# INFLUENCE OF TREE SPECIES RICHNESS ON ARTHROPOD COMMUNITY PATTERNS AND FOLIAR HERBIVORY PLUS ALLOMETRIC EQUATIONS TO PREDICT TREE BIOMASS

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I dedicate this thesis to my grandfather, Luciano, and to my mother, Annamaria. To the former, for showing me the magic of Nature, and to the latter, because without her support and love, I would be a homeless freak.

# INFLUENCE OF TREE SPECIES RICHNESS ON ARTHROPOD COMMUNITY PATTERNS AND FOLIAR HERBIVORY PLUS ALLOMETRIC EQUATIONS TO PREDICT TREE BIOMASS

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# CONTENTS

# SUMMARY

This PhD thesis investigates the mechanisms shaping arthropod communities and the herbivory damage they cause. Because links among trophic levels are an important part of biodiversity–ecosystem functioning relationships, I looked on how tree species richness influenced different group of arthropods and different kind of foliar damage in a species-rich subtropical forest in China. One part of this thesis was also dedicated to the construction of allometric equations to predict tree biomass.

In **chapter one**, I used 27 forest plots established in a subtropical Chinese forest to investigate the links between tree species richness, tree phylogenetic diversity and tree species composition with herbivory damage on leaves caused by the main arthropod feeding guilds, namely leaf chewers, leaf skeletonizers and sap-suckers. I found that increasing tree species richness and phylogenetic diversity increased the amount of damage. However, the tree species richness effect on herbivory damage occurred only at low phylogenetic diversity. Tree species with the lowest relative leaf biomass (proportion of the total leaf biomass within a plot) suffered highest damage. The amount of damage provoked by the different feeding guilds was differently influenced by tree species identity, tree species richness, and tree species relative leaf biomass. I could not observe a reduction of herbivory damage by predators in plant species–rich plots; my results rather supported bottom-up hypotheses relying on resource dilution, which differentially affected the different arthropod feeding guilds.

In **chapter two**, I trapped and sorted arthropods that were living in the canopy and in the understory of the same plots as those used in chapter 1. I captured 28’198 individuals that we assigned to different feeding guilds (herbivores, predators, pollinators, and detritivores). I related the abundance and species richness of these arthropods to tree species richness to

investigate which one of a set of well-known ecological hypotheses was likely shaping arthropod communities. Arthropod abundance increased with plant species richness and arthropod species composition depended on stand age. The separate feeding guilds were not related to tree species richness but positive relationships between the predators and the other feeding guilds were observed. These results were in accordance with a general bottom-up influence from the plant community to higher trophic levels, as predicted by the More Individuals Hypothesis, and no top-down control on herbivore arthropods.

In **chapter three**, I developed allometric equations to predict the biomass of eight common tree species found in South-East China. We felled 154 trees and accurately measured their biomass by compartment (leaf, branch wood, stem wood, dead attached material, and roots). Biomass allometric equations fitted on log-log scale explained generally more than 90% of data variability. Different biomass compartments were differently variable and required different models to be accurately predicted; hence I suggested different predictors and models to use. Finally, I also provided a concrete example on how to use the models to predict the biomass of whole tree sections.

To summarize, I demonstrated that arthropod community patterns and arthropod foliar herbivory were shaped by bottom-up forces. Tree species richness was a significant factor in explaining these patterns. I also provide a complete set of allometric models and instructions on how to use them to predict in detail the biomass of eight tree species.

# ZUSAMMENFASSUNG

Diese Doktorarbeit untersucht die Mechanismen, welche Arthropodengemeinschaften formen und die Herbivorieschäden, die diese Gemeinschaften verursachen. Da die Verbindungen zwischen trophischen Ebenen ein wichtiger Bestandteil der Beziehungen zwischen Biodiversität und Ökosystemfunktion sind, habe ich in einem artenreichen subtropischen Wald in China untersucht, wie der Baumartenreichtum verschiedene Gruppen von Arthropoden und verschiedene Arten von Blattschäden beeinflusst. Ein weiterer Teil dieser Arbeit widmet sich der Konstruktion von allometrischen Gleichungen, um Baumbiomasse voraussagen zu können.

Im **ersten Kapitel** habe ich anhand von 27 Untersuchungsflächen in einem subtropischen chinesischen Wald die Beziehungen zwischen Artenzahl, phylogenetischer Diversität und Zusammensetzung der Baumgemeinschaften und den durch Herbivore verursachten Blattschäden untersucht. Dabei habe ich zwischen den Schadmustern der häufigsten Herbivorengilden unterschieden und Blattschäden verursacht durch kauende Insekten, Blattskelettierer und Pflanzensaftsaugern analysiert. Ich habe herausgefunden, dass eine erhöhte Baumartenzahl und höhere phylogenetische Diversität der Baumgemeinschaften den Blattschaden erhöhen. Der Effekt von Baumartenzahl auf Herbivorieschäden trat allerdings nur bei geringer phylogenetischer Diversität auf. Baumarten mit der geringsten relativen Blattbiomasse (Anteil der Gesamt-Blattbiomasse einer Versuchsfläche) wurden am stärksten geschädigt. Das durch die verschiedenen Herbivorengilden verursachte Ausmass der Schäden wurde unterschiedlich von der Identität, der Artenzahl und der relativen Blattbiomasse der Baumarten beeinflusst. In artenreicheren Versuchsflächen konnte ich keine Verminderung von Herbivorieschäden sehen. Meine Resultate unterstützen daher eher ‚bottom-up' Hypothesen, welche sich auf Ressourcenverdünnung stützen, die dann auf die verschiedenen Herbivorengilden unterschiedlich wirkt.

Im **zweiten Kapitel** habe ich Arthropoden aus Baumkronen und Unterholz von den gleichen Versuchsflächen wie denjenigen aus Kapitel 1 eingefangen und sortiert. Ich habe 28'198 Individuen gefangen, welche anschliessend verschiedenen Ernährungsgilden (Herbivoren, Räuber, Bestäuber und Detritivoren) zugewiesen wurden. Ich habe die Abundanz und Artenzahl dieser Arthropoden zur Baumartenzahl in Beziehung gesetzt, um herauszufinden, welche ökologische Hypothese am ehesten die Arthropodengemeinschaften erklärt. Die Abundanz der Arthropoden stieg mit der Artenzahl der Bäume an, während die Artenzusammensetzung der Arthropoden abhängig vom Bestandsalter der Untersuchungsflächen war. Die einzelnen Ernährungsgilden zeigten keinen direkten Bezug zur Baumartenzahl, aber es gab eine positive Beziehung zwischen den Räubern und den anderen Ernährungsgilden. Diese Resultate sind in Übereinstimmung mit einem allgemeinen ‚bottom-up' Einfluss der Pflanzengemeinschaften auf höhere trophische Ebenen, wie dies von der „Mehr Individuen Hypothese" vorausgesagt wird. Eine ‚top-down' Kontrolle auf pflanzenfressende Arthropoden konnte ich hingegen nicht feststellen.

Im **dritten Kapitel** habe ich allometrische Gleichungen entwickelt, um die Biomasse von acht häufigen Baumarten aus Südostchina vorauszusagen. Wir fällten 154 Bäume und bestimmten die Biomasse der einzelnen Baumbereiche (Blatt, Astholz, Stammholz, totes Material und Wurzeln). Die allometrischen Gleichungen, angepasst an die log-log Skala, erklärten im Allgemeinen mehr als 90% der Datenvariabilität. Die Biomasse der einzelnen Baumbereiche war unterschiedlich variabel und benötigte unterschiedliche Modelle, um genau vorausgesagt werden können. Deswegen habe ich verschiedene Prädiktoren und Modelle vorgeschlagen. Schliesslich stelle ich noch ein konkretes Beispiel vor, das zeigt wie man diese Modelle anwenden kann, um die Biomasse von ganzen Baumbereichen vorauszusagen.

Insgesamt zeigt meine Arbeit, dass die Struktur von Arthropodengemeinschaften und die Blattschäden durch Herbivorie von ‚bottom-up' Kräften geformt werden. Baumartenzahl war ein signifikanter Faktor, um diese Muster zu erklären. Ausserdem stelle ich ein komplettes Set von allometrischen Modellen zur Verfügung; inklusive Erklärungen zur Anwendung dieser Modelle, um die Biomasse von acht Baumarten im Detail vorauszusagen..

# GENERAL INTRODUCTION

Biodiversity–ecosystem functioning (BEF) studies have gained a lot of attention since the world has been recognized to face the sixth mass extinction in its history (Totten, Pandya, and Janson-Smith 2003; Wake and Vredenburg 2008). Forests are one of the most important terrestrial ecosystems, containing more than half of the terrestrial animal and plant species (FAO 2011). In addition, forests are crucial actors of the global carbon cycle (Phillips et al. 2008; Schimel 2014), in providing services for people such as fuel and food (Aerts and Honnay 2011; Chiabai et al. 2011; Ferraro et al. 2011), and as biodiversity hotspots (Barthlott et al. 2005). One key component of forest functions is the diversity of species living therein (Scherer-Lorenzen, Körner, and Schulze 2005). Plant biodiversity is entangled with forest functions, influencing the production of biomass and the stability of the system, and supporting fauna and biochemical cycles (Scherer-Lorenzen, Körner, and Schulze 2005). However, despite the importance of forests, and in particular tree species-rich forests, fewer BEF projects have studied these ecosystems compared with grassland or microcosm ecosystems (Balvanera et al. 2006; Nadrowski, Wirth, and Scherer-Lorenzen 2010), probably because of difficulties in gathering data for forest ecosystems.

Yet, a question still pending in ecology, and which is intimately linked with biodiversity effects on ecosystem functioning, is how such a high number of species can coexist in a limited spatial area. This question is essential to understand the functioning of the ecosystem and has been a central point to many BEF studies. To help answer this question, the mechanisms controlling plant and animal populations must be investigated. Therefore, the main purpose of this thesis is to study one aspect of species coexistence: the mechanisms linking the plant community with arthropod communities.

*Mechanisms sustaining plant diversity: herbivory*

Among the different mechanisms that have been proposed to explain how relatively similar species could coexist, an important one relies on density-dependent effects. The more an organism is abundant, and thus present in higher concentrations, the more it experiences predation from predators, becomes infected by pathogens, or gets eaten by herbivores (the Janzen-Connell hypothesis, Janzen 1970; Connell 1971). This negative consequence of being abundant provides a competitive advantage to the less abundant species and therefore contributes to the maintenance of plant species diversity (Coley and Barone 1996; Mulder et al. 1999; Whiles and Charlton 2006; Stein et al. 2010; Bagchi et al. 2014). Such density-dependent mechanisms have been shown to impact seedling recruitment (Bagchi et al. 2014), plant growth and plant biomass (Kim, Underwood, and Inouye 2013; van Mölken et al. 2014), and growth and density of plant populations (Kim, Underwood, and Inouye 2013). Applied to forests, species-rich stands should suffer less herbivory than species-poor forests since the former have less conspecific individuals per unit area. This phenomenon was observed and proved in simple systems, such as crop fields and in forest mixtures containing 2–3 tree species (reviewed by Jactel & Brockerhoff 2007 and Cardinale et al. 2011). However, contrasting patterns were obtained in species-rich forests (Schuldt et al. 2010). Recently, other measures of species diversity have been proposed as being more important than species richness. For instance, measurements quantifying how much each plant species differs from others might be of primary importance because the number of species matters only if these species are different in the view of their consumers (Jactel and Brockerhoff 2007; Castagneyrol et al. 2014). In this regard, phylogenetic diversity, which describes the evolutionary linkage among species, and functional diversity, which describes the differences in traits among species, have been recognized as important factors that mediate the effects

of plant species richness on herbivory (Dinnage 2013; Castagneyrol et al. 2014; Schuldt et al. 2014). However, these earlier studies were performed on tree saplings or in grasslands. The present study for the first time addresses the question of herbivory in the tree canopy in relation to tree species richness and phylogenetic diversity in a species-rich forest. Because the canopy contains a great amount of resources and consumers (Basset et al. 2003) and is essential for biomass production (Margaret D Lowman 2009), a thoughtful investigation was worthwhile to undertake. Hence, my main goal in chapter one was to test if high plant species richness is related to reduced leaf herbivory, particularly in the canopy layer.

*Mechanisms shaping arthropod populations: bottom-up or top-down?*

Arthropods are an important phylum accounting for 1'170'000 described species, which constitutes more than 80% of all living animal species (Thanukos 2015). In forests, they are the most abundant group of herbivores and they are responsible of the highest estimated herbivory impact (Schowalter 1986; M D Lowman and Moffett 1993). Arthropods are also essential providers of services mandatory for the functioning of the ecosystems such as litter decomposition (Brussaard 1997), nutrient transfer (Seastedt and Crossley 1984; Belovsky and Slade 2000), and pollination (Axelrod 1960). In particular, herbivorous arthropods have a pivotal role as they feed on the primary producer group, the plants, and they are themselves an important food source for the higher trophic levels. Despite their recognized importance in ecosystem functioning little is known about the mechanisms regulating arthropod populations in species-rich forests.

There are two general directions for the different hypotheses concerning arthropod population regulation: bottom-up and top-down. Bottom-up hypotheses postulate that the lower level, the producers, shape the primary consumer communities which in turn shape

their predator communities. Top-down hypotheses instead postulate that predators or herbivores shape the communities on which they feed. The most common hypotheses and the direction of their action are schematized in figure 1 of chapter 2. Because these different hypotheses make distinct predictions, it is possible to observe the arthropod and the plant communities, to quantify them, and to deduce which predictions and thus which hypotheses are best matched. For example, the enemy hypothesis predicts that in plant species-rich areas a high abundance of predators reduces the abundance of herbivores (Paine 1969; Root 1973; Hunter and Price 1992). To confirm such a top-down control mechanism, we expect to observe a positive relationship between plant species richness and predator arthropods and a negative relationship between predator arthropods and herbivore arthropods. In contrast, a bottom-up control hypothesis, such as the resource concentration hypothesis, predicts a greater herbivore species richness in relation to a greater plant species richness, because the resources dilution should prevent any arthropod population from becoming dominant (Root 1973). A general understanding of the forces shaping the arthropod communities is still far from being achieved (Cardinale et al. 2011). Publications having opposite conclusions (e.g. Siemann et al. 1998 vs. Schuldt et al. 2011) further intensify the doubts and debate.

*Study site: the comparative study Plots (CSP's)*

The region where this study was conducted is located in Zhejiang Province, southeast China (Fig. 1). The climate is subtropical, characterized by dry winters, warm summers, and by a monsoon regime with rain falling mainly in May and June and reaching a yearly total of ca. 2000 mm (Geißler et al. 2012). The average annual temperature is 15.3 °C (Yu et al. 2001).

The chapters one and two of this thesis — leaf herbivory damage and arthropod populations — were conducted in the Gutianshan National Nature Reserve in Kaihua County, Zheijiang

Province (Fig. 1). This reserve was established in 1975 to protect the old evergreen broad-leaved forest. The reserve contains 57% natural secondary forest aged up to 180 years. The plant species richness is very high: 1462 seed plant species of which over 250 are woody. The high vascular plant richness of this whole region qualifies it as a "phytodiversity hotspot" (Barthlott et al. 2005). The site location is also of interest because subtropical forests are an important part of the world's forests, covering 3.3 millions of squared kilometers (Lindquist et al. 2012). This type of forest was covering large parts of China (Wu 1980), but it is now suffering of strong anthropogenic pressure (Wang, Kent, and Fang 2007).


Fig. 1. Left panel, location of the study site in China (orange balloon) in Zhejiang Province (red). Right panel, the Gutianshan National Nature Reserve (delimited in orange) with the different comparative study plot locations (red dots). Images from BEF China project (www.bef-china.de).

*Allometric equations to calculate biomass*

Among the different aspects of BEF studies, the biomass and the biomass production are central measures to quantify ecosystem performance (Tilman, Wedin, and Knops 1996; Cardinale, Ives, and Inchausti 2004; Balvanera et al. 2006; Baruffol 2014). Additionally,

nowadays biomass has gained a lot of attention because half of it is made out of carbon, one of the main factors contributing to climate change (IPCC 2007). In this regard, forests have been recognized as sink, reservoir, or source of carbon (Phillips et al. 2008; Schimel 2014). However, in contrast to grasslands, measuring forest biomass is extremely difficult. Direct measurements are logistically complex and expensive because of the weight and the size of the trees. Direct measurements are also destructive, therefore making the possibility to perform repeated measurements on the same individual impossible. To overcome these problems, different allometric equations were developed for numerous forests located in various parts of the world (Chave et al. 2014). Allometric equations have the advantage of relating easily measurable tree traits, like the diameter at breast height or the tree height, to biomass. Allometric equations exist in a variety of forms and complexity. Because the debate on the best equations to use is still ongoing (see Chave et al. 2014), we decided to build our own set of allometric equations. Taking the opportunity to fell trees in a forest that was undergoing clear-cut anyway and that was situated in the same region as is the Gutianshan National Nature Reserve, we developed different equations describing the total biomass and the biomass of the different tree compartments (leaves, branch wood, stem wood, dead attached material (DAM) and roots).

**Thesis outline**

This PhD thesis investigates the mechanisms shaping the arthropod communities and herbivory damage from a biodiversity–ecosystem functioning perspective. One part of this thesis was also dedicated to the construction of allometric equations to predict tree biomass.

In the **first chapter**, I investigate if and how tree species richness influences tree foliar herbivory damage. First, I look at the effects of tree species richness and phylogenetic diversity at the level of the whole tree community, i.e. as if the plots were unique and undifferentiated entities. Then, I investigate if the different tree species suffer different levels of herbivory in relation to tree species richness. Furthermore, I identify the type of herbivory on leaves, namely chewing, skeletonizing or sap-feeding damages, and examine if these damages are differently influenced by tree species richness, tree phylogenetic diversity, and tree species identity.

In the **second chapter**, I focus on the arthropod communities. I investigate how abundance and species richness of the different feeding guilds (herbivores, predators, pollinators, and detritivores) are linked among themselves and with tree species richness. I pay special attention to the herbivore and the predator communities in order to reveal which hypothesis most likely explains the observed patterns. The main goal is to understand if the herbivores are more influenced by their predators (top-down control) or by their resources (bottom-up control).

In the **third chapter**, I build allometric equations to predict detailed biomass values for the whole tree and for the different biomass compartments of the tree. I also investigate which

predictors are the most useful in reducing the bias and improving the model's fit in order to enhance the quality of biomass predictions. Furthermore, I provide a concrete example of how to use these equations to predict the biomass of a whole plot.

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# CHAPTER 1

# Feeding guild-specific effects of tree species richness on herbivory in a subtropical forest canopy

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# Feeding guild-specific effects of tree species richness on herbivory in a subtropical forest canopy

**Abstract**

*Plant species richness has been linked to arthropod herbivory damage and the latter, in turn, has been linked with maintenance of plant species diversity. Yet, these links are poorly understood and have mainly been studied in grasslands or in artificial tree plantations with low species richness. Furthermore, most of the studies provide results on newly established experiments, where trophic links are not fully established, or on tree saplings, therefore ignoring what happens in the canopy.*

*We used 27 forest plots established in a subtropical Chinese forest in order to investigate the links between tree species richness, tree phylogenetic diversity and tree species composition with leaf total herbivory damage and the leaf damages caused by the main arthropod feeding guilds, namely leaf chewers, leaf skeletonizers and sap-suckers.*

*We found that the amount and the type of herbivory damage were influenced by tree species richness and tree phylogenetic diversity. Increasing tree species richness and tree phylogenetic diversity increased the amount of damage. Furthermore, the strongly positive tree species richness effect on herbivory damage occurred only at low phylogenetic diversity. The relative leaf biomass of particular species (proportion of the total leaf biomass within a*

*plot) affected herbivory damage: tree species with the lowest relative leaf biomass suffered most damage. The damage caused by different feeding guilds was differentially affected by tree species richness, tree species identity, and tree species relative leaf biomass.*

*Our results do not support the hypotheses predicting a better herbivore control by predators or a difficulty for herbivores to forage with increasing plant species richness. The interaction of tree species richness with tree phylogenetic diversity showed that herbivory damage increased with tree species richness only at low levels of phylogenetic diversity, that is, when tree species are relatively similar. Such result supports the diet mixing hypothesis where generalist herbivores take advantage of a species-rich diet. On the other hand, that tree species with low relative leaf biomass experienced more herbivory damage likely reflected an accumulation of specialist herbivores.*

*Large differences in herbivory damage among tree species together with effects of tree species richness act on the ecosystem via varying selective pressures and therefore have the potential of being an important mechanism for the maintenance of plant biodiversity and species composition.*

**Introduction**

In the context of biodiversity–ecosystem functioning (BEF) studies, foliar herbivory is thought to be important because it affects ecosystem processes, plant species richness and plant species composition (Coley & Barone 1996; Mulder et al. 1999; Whiles & Charlton 2006; Stein et al. 2010; Bagchi et al. 2014). For instance, foliar herbivory can influence

seedling recruitment (Bagchi et al. 2014), plant growth and plant biomass (Kim et al. 2013; van Mölken et al. 2014) or growth and density of plant populations (Kim et al. 2013).

Plant species diversity, in turn, is also hypothesized to affect levels of insect herbivory. However, our knowledge on this topic is incomplete and comes mostly from experiments conducted in grasslands (Cardinale et al. 2011). Most of the studies looking at herbivory in forests were carried out in species-poor forests (mostly two- or three-species mixtures, reviewed by Jactel & Brockerhoff 2007) or only saplings were sampled (Schuldt et al. 2010). Little is known about processes occurring in forest canopies of established semi-natural forests, although this stratum is crucial for biomass production (Lowman 2009) and contains a great amount of resources and consumers (Basset et al. 2003). An explanation for this lack of studies is certainly the difficulty to reach the canopy (Barker & Pinard 2001). Moreover, studies linking foliar herbivory to tree species richness did not produce a consistent pattern: higher tree species richness has been linked with lower (Jactel & Brockerhoff 2007; Castagneyrol et al. 2014), higher (Schuldt et al. 2010) or unchanged herbivore damage (Vehviläinen et al. 2007).

Recent studies highlighted the complexity of herbivory-driving factors, and even though plant species richness remains a potentially important factor, other types of diversity effects may complement or even overrule effects of plant species richness. Herbivory has been linked to plant species composition (Jactel & Brockerhoff 2007) or to the presence and absence of particular plant functional groups (Loranger et al. 2013). Additionally, plant phylogenetic and functional diversity are recognized as important factors influencing herbivory (Dinnage 2013; Castagneyrol et al. 2014; Schuldt et al. 2014). The herbivores themselves are playing a major role in this herbivory damage outcome and the above-

mentioned biodiversity patterns have different outcomes depending on the herbivores' foraging preferences (Castagneyrol et al. 2014). Looking at these mechanisms a bit more in detail, the actual theory postulates that the different aforementioned factors act by increasing or decreasing herbivore resource finding or consumption efficiency and that this outcome depends on how broad the herbivore diet range is.

Increasing plant species richness is thought to increase the difficulty for a specialized herbivore to find a suitable host because these are more diluted (the Resource Concentration Hypothesis (Root 1973)). In contrast, generalist herbivores should not be (or be less) sensitive to resource dilution and might even profit directly from more plant species available through resource complementarities (the Dietary Mixing Hypothesis after Bernays et al. (1994)), or indirectly by an increased amount of biomass available (Loranger et al. 2013). Given that many specialized arthropods are not strictly monophagous (i.e. not only feed on a single plant species) but rather feed on a number of related plant species (Ødegaard et al. 2005; Gossner et al. 2009; Futuyma & Agrawal 2009), the phylogenetic or the functional diversity of a plot might be of primary importance. For a given number of plant species, a high phylogenetic (or functional) diversity reduces the number of suitable hosts for specialized herbivores. In contrast, a low phylogenetic diversity (for example, plants of the same genus) would result in high host availability for a herbivore specialized on this particular genus (Dinnage 2013). Hence, phylogenetic and functional diversity are thought to be mediators of species richness: diversity effects should be the strongest when the plant species are the most different, by traits, i.e. functional diversity, or by evolutionary distance, i.e. phylogenetic diversity (Dinnage 2013; Castagneyrol et al. 2014; Schuldt et al. 2014). Castagneyrol et al. (2014) showed that plant species richness influenced specialized arthropods but that for generalist herbivores, this resource dilution effect only occurred

when plant phylogenetic diversity was large. Therefore, final herbivory levels depend on the diversity (broad sense) of the producer level and the degree of specialization at the consumer level.

Additionally, plant species richness has been hypothesized to act indirectly in a negative way on herbivore populations, through an increase of predator abundance (the Enemy Hypothesis (Root 1973), or in a positive way through an increase of plant biomass (the More Individuals Hypothesis (Wright 1983; Srivastava & Lawton 1998). Although the Enemy Hypothesis was demonstrated in simple crop fields (Root 1973; Russel & Edmund 1989; Siemann et al. 1998), scarcely any evidence could be found in more complex species-rich ecosystems (Riihimäki et al. 2005; Vehviläinen et al. 2006; Schuldt et al. 2011). Plant species richness has a positive effect on plant biomass production (Tilman et al. 2001; Cardinale et al. 2007) and this has been shown to be true at our study site (Baruffol et al. 2013). Such increased biomass could affect the abundance of herbivores and therefore the amount of biomass consumed (Loranger et al. 2013). In our study plots plant diversity and total biomass were partially confounded (Barrufol et al. 2013) but the remaining variation was sufficient to test for the specific effects of this additional variable.

In order to investigate which mechanisms are most likely occurring in the canopy of a species-rich subtropical forest, we took advantage of 27 comparative study plots varying in tree species diversity that were set-up within the BEF China project (http://www.bef-china.de, see methods). Attempting to disentangle general plant diversity effects from plant species identity and composition effects, we first looked at the plots as communities, i.e. as a whole and undifferentiated entity. For that purpose, we used a tree selection strategy respecting the proportion of the tree species present in each plot. Secondly, we looked at species-level differences in herbivory damage for the most common tree species within

plots. Thirdly, we looked at the effect of tree species composition *per se* by investigating through multivariate analyses if the plant species matrices correlated with herbivory. Few studies so far have included feeding guilds in their herbivory assessment (Andrew et al. 2012) despite the potential importance of making such a distinction. Since the different feeding guilds may damage plants to different extent (see Vehviläinen et al. 2007) and can react in different ways to plant diversity (Castagneyrol et al. 2013), we not only recorded total leaf damage but also the different feeding guild contributions to this leaf damage.

We built a series of models having tree species richness as main explanatory variable. These models investigated the total herbivory at community level down to the detailed feeding guild herbivory at the tree species level. At the community level (plots as a whole), we additionally looked if the amount of biomass available to folivore arthropods, i.e. estimates of leaf biomass, could help to explain the observed variation in herbivory damage. We also fitted tree phylogenetic diversity in order to test if this component of diversity was better than, or interacting with, tree species richness in explaining herbivory levels. At the tree species level, we additionally analyzed the relative leaf biomass of the most common tree species in each plot to test a potential "dilution effect"; that is, we explicitly looked if the species that were less "available" experienced more or less herbivory.

Leaf toughness has been shown to reduce herbivore performance (Clissold et al. 2009) and to influence herbivory (Coley & Barone 1996; Kursar & Coley 2003). Specific leaf area (SLA) has also been shown to influence herbivory (Neves et al. 2010). These phenotypic traits can vary among trees of the same species and influence herbivory levels (Suomela & Ayres 1994; Ruhnke et al. 2009). Therefore, we included these two variables in the species–level analysis to see if they were related to herbivory differences within tree species. Finally, we included

the branch height in our models because it has been shown to be an important factor (Coley & Barone 1996), with the lower canopy parts having higher herbivory damage than the higher parts. In order to know if this was also true for our forest plots, we sampled branches at varying height. This strategy might also be useful to extrapolate for the part of the canopy that we could not reach.

The different models were designed to answer five questions.

At the community level, we asked: 1) is tree species richness linked with total herbivory damage? and 2) are the different feeding guilds causing different amount of damage and is tree species richness linked with these amounts of damage? In addition we asked the following extra question: are the total amount of leaf biomass and the phylogenetic diversity important in explaining the tree species richness effects in questions 1 and 2? Furthermore we asked 3) is tree species composition linked with total damage or with the damage of specific feeding guilds? At the species level, we asked the following questions: 4) do the different common tree species experience different amounts of total herbivory damage and is this damage linked with tree species richness? and 5) are the feeding guild damages different among the common tree species and is tree species richness affecting these damages? At this level we added the extra question: is the relative leaf biomass of the common tree species within plots related to the total and the different feeding guild herbivory damages?

We hypothesize that tree species richness decreases the overall amount of herbivore damage, although phylogenetic diversity or total leaf biomass might change the magnitude

of the effect. The different tree species should have different amounts of herbivore damage, in part because of their relative abundance (resource concentration hypothesis), and in part because of differences in their leaf characteristics. Because the different herbivore feeding guilds might have different degrees of host specialization and different sensibility to the relative abundance of tree species, to the tree species richness or to the leaf quality, we expect to find varying amounts of damage caused by them.

## Methods

### *Study site*

The study was conducted between the end of June and mid-August 2010 in the Gutianshan National Nature Reserve in Kaihua County, Zheijiang Province, China (29°8’18’’-29°17’29’’ N, 118°2’14’’-118°11’12” E). The terrain is mountainous and ranges in altitude from 250–1260 m above sea level. The climate is subtropical with a monsoon regime; rain falls mainly in May and June and reaches a yearly total of ca. 2000 mm (Geißler et al. 2012). The average annual temperature is 15.3 °C (Yu et al. 2001). The forest contains a majority of evergreen broadleaf woody plant species, followed by deciduous broadleaf and some coniferous species (Yu et al. 2001). Due to anthropogenic disturbances, the forest contains areas of different age and successional stages. Our 27 study plots were classified into five age classes: 1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr, 5, ≥ 80 yr). The plots of 30 × 30 m were established in 2008 within the BEF China project (www.bef-china.de) following a design that attempted a good representation of the different successional stages and different species richness levels, (25-

69 species per plot). Additional information on plot selection and characteristics can be found in Bruelheide et al. (2011).

*Sampling strategy*

As the aim of our study was to sample specifically the canopy, we restrained our candidate plant individuals to the tree species reaching the canopy. A diameter at breast height (DBH) of 10 cm was used as threshold and only trees with a greater DBH were considered. Within the BEF-China framework, all the trees with a DBH >10 cm were measured and identified to the species level (Baruffol et al. 2013). According to this definition, 67 species were identified, 36 evergreen broadleaf, 28 deciduous broadleaf and 3 evergreen coniferous. The species richness within plots of these canopy trees ranged from 3 to 21 species.

To best represent the plot as a community and to have sufficient replication, we sampled 20 trees per plot whenever they were present. If fewer trees were available, we sampled all of them. Four individuals of the species having the greatest number of individuals within the plot were chosen (i.e. four individuals for each of the five most dominant species). In most of the plots, species with fewer individuals were included in order to reach 20 sampled trees. Those additional species were chosen in function of their abundance: the species with most individuals were selected. If some species had the same number of individuals, the species with the greatest total basal area was chosen. Within tree species, individuals were chosen at random. With this strategy, a number of trees representing on average 40% of the total basal area in each plot (ranging from 13% to 85%) was sampled.

On each tree, and when a visual inspection indicated that the crown was long enough to do so, three branches at different height within the canopy were cut with a tree pruner

mounted on interlocked 2–m poles. For trees having a short crown, only two branches were taken and in some cases, only one branch; this was also true for trees being too high and where only the lowest part of crown could be accessed. In the best cases, branches located at ca. 15–16 m above the ground could be reached. To account for within-branch variability, several twigs with about 5–10 leaves were taken; this generally led to 20–30 leaves per branch. For the coniferous tree species, 3–4 twigs per branch were sampled and herbivory was scored for the whole twig. Twigs of *Cunninghamia lanceolata* are flat; they were scanned and processed similarly to the broad leaves of angiosperm trees (see below). Twigs of *Pinus massoniana* and of *Pinus taiwanensis* could not be scanned; herbivory scoring was thus performed shortly after collection.

*Herbivory scoring*

Damage by arthropod herbivores was quantified by a visual scoring process validated within the BACCARA project (www.baccara-project.eu). In brief, leaves were scored by assigning the amount of photosynthetic tissue removed into damage classes: 0%, 1–5%, 6–15%, 16–25%, 26–50%, 51–75% and > 75%. Different types of damage were recognized and were assigned to different feeding guilds: leaf chewers, leaf skeletonizers, sap-feeders, leaf rollers and gall makers. Arthropod damage with unclear origin was marked as “undefined”. A separate herbivory score for each feeding guild and a total herbivory score were estimated for each leaf. The median value of each score was then used for the analyses. In order to prevent biases, a single person (MB) performed the whole herbivory assessment. Furthermore, the first 20% of the processed leaves were re-scored and this process was run until less than 10% of the leaf scores had to be modified. Such a procedure corrected for the evolution of leaf damage perception by the observer.

*Phylogenetic tree diversity and leaf biomass*

In order to test the hypotheses regarding the dilution effect, effects of tree phylogenetic diversity and of biomass availability, several co-variables were included in the analyses (see Table 1).

Leaf biomass was estimated with three separate allometric models for broadleaf evergreen, broadleaf deciduous and coniferous tree species. These models scaled leaf biomass with DBH and were obtained from another study conducted in the same area: 154 trees ranging from 1 to 37.5 cm DBH were felled and their leaf biomass accurately measured (personal data). The measured trees belonged to eight species: *Cunninghamia lanceolata* and *Pinus massoniana* (coniferous, 36 individuals); *Castanopsis fargesii*, *Castanopsis sclerophylla* and *Schima superba* (broadleaf evergreen, 62 individuals); *Alniphyllum fortunei*, *Liquidambar formosana* and *Sassafras tzumu* (broadleaf deciduous, 56 individuals). The DBH range of the trees used to produce the allometric models was close to the DBH range of the trees found in the study plots: only 3.7% of the study plot trees had a DBH > 40 cm.

Total plot leaf biomass was calculated as the sum of the predicted leaf biomass of all the trees with a DBH > 10 cm within the plot. The coefficients of variation of the total plot leaf biomass calculated according to Chave et al. (2014) ranged from 16% to 43%. These uncertainties are relatively high because the leaf biomasses were very variable, even among individuals of the same species. The sum of all the individual leaf biomasses belonging to one species was divided by the total plot leaf biomass to obtain a measure of tree species relative leaf biomass within each plot. This procedure was applied to the nine most common tree species (see below).

Tree species phylogenetic diversity of each plot was also calculated using all the trees with a DBH > 10 cm. The phylogenetic data were acquired from an ultrametric phylogenetic tree of the tree species found in the 27 study plots (Michalski & Durka 2013). The coniferous and some rare species had to be excluded from the calculation because data were lacking. Phylogenetic diversity (PD) was calculated by summing the phylogenetic tree branch lengths according to the method of Petchey and Gaston (2006). PD was closely correlated with tree species richness and stand age (Pearson correlation 0.96 and 0.68, respectively). The phylogenetic diversity is a plot-level value based on species-level variables (see Table 2). In order to investigate the effect of two important morphological leaf traits, specific leaf area (SLA) and leaf toughness (Pérez-Harguindeguy et al. 2003; Eichhorn et al. 2007; Kitajima & Poorter 2010) at population level, i.e. trait variation within species among plots, we measured ten randomly chosen healthy leaves per species per plot. Leaf toughness was defined as the force required to pierce the leaf with a standard needle (mN), the average of the ten leaves was taken as the value for this tree population. The SLA was obtained by scanning and measuring the area of the 10 fresh leaves, then dividing the sum of their area by the sum of their dry weight ($cm^2/gr$).

*Statistical analysis*

Because no variables were measured at leaf level, leaf herbivory damage was averaged at the branch level. Heteroscedasticity of the residuals was removed by applying a log(Y+1) transformation. The different models (see below) had a structure and incorporated variables that reflect the questions we were asking. A great number of covariates or high-order interactions were deliberately not included (as they would increase the type I-error probability). All models included the sampling date (treated as a block effect), the stand age

and the tree species richness. Stand age was used by Bruelheide et al. (2011) as a factor with the major influence on variables such as plant biomass or tree height and was thus included in all our models. Sampling date can mathematically only increase the amount of herbivory damage on one leaf and therefore we controlled its effect by putting this term at the beginning of the models. Depending on the model, several further explanatory variables were added (see below). We retained in minimal models the additional terms and interactions related to the question asked and the terms and interactions that were significant. The order of variables in the models was based on the given hierarchy: first plot-level, then species-level, then population-level, then individual-level and finally branch-level variables (see also Table 2). Plot-identity and individual identity were used as random-effects terms, that is, as error terms for testing fixed effects at the corresponding level of the given hierarchy. Branch identity was incorporated as a random-effects term for models including the herbivore feeding guilds (several measures on each branch) and tree species identity for the models implying tree species. The statistical program R 3.0.1 was used for all the analyses (Core Team R Development 2012). Mixed effect models were run with ASReml for R (Gilmour et al. 2009) and multivariate analyses were performed with the package “vegan” for R (Oksanen et al. 2012).

*Community-level analysis*

Total leaf herbivory damage at the plot level was investigated with the following model 1:

1) *Log(percent damage+1) ~ Date+(Age*SR)*Height*

Here the *-sign indicates factorial multiplication, i.e. A*B = A+B+A×B, where A×B is the interaction term between A and B.

Model 2 was used to investigate the amount of feeding guild damage at the plot level:

2) *Log(percent damage+1) ~ Date+(Age*SR)*Feed*Height*

Besides the three-way interaction "SR×Age×Feed", higher than two-way interactions were excluded from the analysis. In order to test the potential effect of total plot leaf biomass, this term was inserted in the minimal models 1 and 2 before the Age and SR terms. We assumed stand age and tree species richness to cause total leaf biomass variation and this assumption was reflected by fitting the total leaf biomass term before the Age and SR terms. The effect of phylogenetic diversity was tested by re-running models 1 and 2 successively with PD fitted before or after controlling for the effects of tree species richness and stand age.

*Species-level analysis*

In order to test the influence of tree species richness on the differences in leaf herbivory damage among tree species, we built a reduced dataset including only species with enough replication; less replicated species would be confounded with plot effects. Nine species were retained as they matched with the replication threshold that we set: to have at least 40 branches sampled and to be present in at least 5 plots. These species were: *Castanopsis eyrei* (cae), *Castanopsis fargesii* (caf), *Castanea henryi* (cah), *Daphniphyllum oldhamii* (dao), *Lithocarpus glaber* (lig), *Myrica rubra* (myr), *Pinus massoniana* (pim), *Quercus serrata* (qus) and *Schima superba* (scs). The sum of their basal area represented between 41 to 100% of

the total plot basal area (except for an outlier plot where they represented only 10% of the total plot basal area).

Model 3 was used to investigate the importance of tree species identity on the total leaf herbivory damage:

3) *Log(percent damage+1) ~ Date+(Age*SR)*(Con+Spec)*(Tough+SLA)*Height*

We considered two-way interactions and the two three-way interactions A*ge×SR×Con* and *Age×SR×Spec*.

Model 4 was used to test if the feeding guild-specific herbivory damage was different among tree species and responded to the tree diversity gradient:

4) *Log(percent damage+1) ~ Date+(Age*SR)*(Con+Spec)*(Tough+SLA)*Height*Feed*

Only interactions up to third order were considered. In order to test for a potential dilution effect, for instance, if the relative leaf biomass of the tree species could explain variation in leaf herbivory damage, final models 3 and 4 were re-run inserting the relative biomass before the Age and SR terms. As for the total leaf biomass, we assumed a causal relationship between tree species identity and relative leaf biomass.

*Multivariate analysis*

In order to test for a potential effect of tree species composition on leaf herbivory damage, the same tree species that we used to calculate the phylogenetic diversity was ordinated through Nonmetric Multidimentional Scaling (NMDS, package "vegan" for R (Oksanen et al. 2012)). This procedure first performs a two dimensions-ordination that automatically chooses the best data transformation for the species scores and axes scaling. The Jaccard dissimilarity index was used for the distance among plots. Second, the explanatory variables were fitted in turn according to their most rapid change and their highest possible correlation in the ordination space. A permutation procedure ($10^5$ times) was used to calculate an empirical p-value (Oksanen et al. 2012). Total leaf herbivory damages and the different feeding guild damages averaged at plot level were tested with this method.

**Results**

*General statistics*

31'249 leaves (or twigs concerning the three coniferous species, see Methods) were measured on a total of 1291 branches. The average amount of photosynthetic tissue removed by herbivores at the plot level was 7.0%, ranging from 4.3% to 11.2%.

The different feeding guilds caused different amounts of damage ($F_{3,76.4} = 139.3$, $P < 0.001$, Fig.1). Leaf rollers and leaf miners were responsible for a negligible amount of damage (together less than 0.4%); for the sake of simplicity they were excluded from the analyses of feeding guild herbivory (but their contribution is included in the total herbivory damage).

*Question 1: is tree species richness linked with total herbivory damage (model1)?*

The minimal version of model 1 led to the ANOVA table shown in Table 3. Tree species richness had a clear positive link with total herbivory damage (Fig. 2, Table 3). This relationship was independent of stand age: the variability explained by tree species richness remained virtually the same controlled or not for stand age. Branch height had a clear effect: with increasing height the leaves were less damaged.

*Question 2: do the different feeding guilds cause different amounts of damage and is tree species richness linked with these amounts of damage (model 2)?*

Model 2 simplification led to the ANOVA tables shown in Table 4. Variables of interest were "Feed" and the following terms. The variables preceding "Feed" were kept in the model to control for their effects.

The different feeding guilds removed significantly different amounts of leaf tissue (Fig. 1, Table 4). Stand age and tree species richness were independent (as in model 1) but not their interaction with feeding guilds (see model 2a vs. model 2b). This is because these two interactions were partially confounded. Hence, the first term removes both the variation the two terms explain together and the variation this term explains exclusively by itself, so that the second term can only remove the variation it explains exclusively by itself. Nevertheless, the interaction of tree species richness with feeding guilds remained significant even when fitted after the interaction of stand age with feeding guilds. Different feeding guild responses to tree species diversity were mainly due to a strong positive richness response of chewers (Fig. 3a). The other feeding guilds showed very little absolute change although herbivory by the sap-sucker feeding guild increased two-fold from low (5 tree species, 0.47% herbivory) to high tree species richness (20 tree species, 0.97% herbivory). Chewers showed a strong

negative response to branch height (from 4.7% herbivory at 1 m to 2.8% at 16 m height) whereas the other feeding guilds showed much weaker responses (Fig. 3b).

*Influence of the total tree leaf biomass at the community level*

Are the total herbivory and the different feeding guild herbivory damages linked with the amount of leaf biomass in the plot? Stand age and tree species richness explained together 64.3% of the leaf biomass variation among plots. The main part of the explanatory power was confounded between the two variables (38.9%): species richness contained only 5.4% of independent information whereas stand age contained 20.0% of independent information. When introduced before stand age and tree species richness in the total herbivory final model (model 1, Table 3), the amount of leaf biomass explained only a marginal amount of variation ($F_{1,21.0} = 3.5$, $P = 0.08$). In addition, the amount of variance explained by stand age and species richness remained virtually unchanged when they were fitted after leaf biomass, indicating that their link with herbivory damage was independent of leaf biomass. Introducing leaf biomass (term in second position in model 2) in the feeding guild analysis removed the significance of the interaction between stand age with feeding guilds but did not change the significance of the interaction of tree species richness with feeding guilds. Leaf biomass was significantly interacting with feeding guilds ($F_{3,\ 66.3} = 5.3$, $P < 0.01$). Together, these results indicate that leaf biomass had an effect that depended on the feeding guild type, because in model 2 significance values changed with its inclusion. This effect was mainly due to an influence of stand age on leaf biomass.

*Influence of the phylogenetic diversity at the community level*

In the models where PD was fitted after SR and Age, SR + Age removed all the variance that PD could explain and the results were similar to the previous results of model 1 and 2. In the models were PD was fitted first, it was highly significant. Because PD and SR were highly correlated, their effects in the models were exchangeable. But notably when PD and SR were fitted before stand age, they produced a significant interaction affecting total herbivory ($F_{1,18.0}$ = 5.7, $P$<0.05). The positive effect of tree species richness on herbivory damage was stronger at low levels of phylogenetic diversity and became inexistent at higher levels of phylogenetic diversity (Fig. 4).

Regarding the different feeding guilds, PD was never significant when fitted after SR. On the other hand, SR was still explaining a significant amount of variance when fitted after PD (PD + SR + Age) and when fitted after PD + Age (Age + PD + SR and PD + Age + SR). Whatever the variable order, there was never a significant interaction of SR with PD with the herbivory damage of the different feeding guilds.

*Question 3: do the different common tree species experience different amounts of herbivore damage and is this damage linked with tree species richness (model 3)?*

The coniferous species *Pinus massoniana* had significantly less herbivory damage than the other tree species and the other tree species were also significantly differently affected among each other by herbivores (Table 5, Fig. 5). Toughness and specific leaf area were not linked with herbivory damage and were thus removed from the final model. There was no interaction between tree species identity and tree species richness (Table 5), indicating that there were no differences in how the different tree species responded to the species diversity gradient with regard to herbivory damage.

Final model 3 was re-run placing the tree species richness term at the end of the model (but still before the interactions). Tree species richness remained significant ($F_{1,21.5}$ = 5.7, $P$<0.05). Such a result means that the plots did experience increasing herbivore damages with increasing tree species richness even when the different herbivory levels of the different common tree species were accounted for and when the effect of branch height (which can vary among plots) was accounted for too.

*Question 4: are the feeding guild patterns different among the common tree species and is tree species richness affecting these patterns (model 4)?*

The coniferous species was impacted differently by the different feeding guilds compared with the broadleaved tree species (Fig. 6). The broadleaved tree species themselves were also impacted differently among each other by the different feeding guilds (Fig. 6, Table 6). The impact of the different feeding guilds was different along the tree species richness gradient between the coniferous and the broadleaved species (Fig. 7) but not among the different broadleaved species (Table 6). Leaf toughness and SLA did not interact with the feeding guilds and were thus not retained in the final model.

*Test of the dilution effect (tree species relative leaf biomass in the plot) on the total and the different feeding guild herbivory damages*

Tree species identity was responsible for 66.7% of tree species relative leaf biomass variation among plots. Fitted before the species identity term (model 3), tree species relative leaf biomass was significant ($F_{1,58.1}$ = 4.5, $P$<0.05, the coniferous species was included with the other species in the model). This relation was negative: tree species with higher leaf biomass within the plot experienced less herbivory damage. This indicates that a part of the

differences in herbivory damage experienced by the different tree species was likely due to a difference in their relative leaf biomasses. However, the tree species identity term kept a large explanatory power even when fitted after relative leaf biomass ($F_{8,82.0}$ = 22.8, *P*<0.001 vs. $F_{8,84.9}$ = 24.4, *P*<0.001 in the model without leaf relative biomass). This indicates that the major part of herbivory damage differences among tree species were independent of their relative leaf biomass.

The species relative leaf biomass had a different impact on the different feeding guilds ($F_{3,181.0}$ = 30.3, *P*<0.001, model 4). The effect of species identity on the damage of the different feeding guilds remained highly significant when controlled for leaf relative biomass ($F_{24,235.0}$ = 28.6, *P*<0.001 vs $F_{24,243.9}$ = 32.7, *P*<0.001 when not controlled for leaf relative biomass). Such results show that whereas a significant part of the effect of species identity on the difference between feeding guild damage was due to the relative leaf biomass, the greatest part of the species identity effect was independent of the relative leaf biomass.

*Question 5: is tree species composition linked with total herbivory or the feeding guild-specific damage?*

Plots ordinated by tree species composition did not correlate with total herbivory damage or the damage of any of the different feeding guilds (all $R^2$ < 0.12, all *P-values* > 0.2). However, tree species composition had a relationship with two variables that were important in explaining leaf herbivory damage. Tree species composition was linked with total plot leaf biomass and with tree species richness ($R^2$ = 0.38, P = 0.004 and $R^2$ = 0.62, P<0.001 respectively).

**Discussion**

Our results support a significant and positive effect of tree species richness (or phylogenetic diversity) on leaf damage caused by herbivores in the canopy. Although one has to be careful on drawing conclusions from observational studies, these provide pictures of natural complex ecosystems that could not be generated experimentally (Leuschner et al. 2009). Therefore, our results are valuable in helping to verify if theoretical predictions from simpler systems are in accordance with real forest conditions. Furthermore, our study is one within few specifically intended to study herbivory in the canopy layer in relation to diversity effects. As ecological conditions are different in the canopy (only a subset of the plant species present in the plot are effectively represented in the canopy, solar radiation is stronger, humidity is lower, wind and temperature variations are greater (Jones 1983; Oke 1987)), it is essential to measure herbivory *in situ* rather than extrapolating from other habitats. It is interesting to note that our results agree in magnitude with what has been observed in natural forests (i.e. (Neves et al. 2010; Schuldt et al. 2010). Such damage levels have been shown to already impact plant fitness (Zvereva et al. 2012).

*Effect of diversity gradients*

The positive effect of tree species richness on leaf damage by herbivores contrasted with the findings of other studies (Massey et al. 2006; Unsicker et al. 2006; Jactel & Brockerhoff 2007; Sobek et al. 2009; Stein et al. 2010), but concurred with others (Mulder et al. 1999; Schuldt et al. 2010; Plath et al. 2011; Dinnage 2013; Loranger et al. 2013; Schuldt et al. 2014). The plant species richness range in the aforementioned studies finding a positive richness effect on herbivore damage (1–3 to 25–68) was not very different form the plant species richness

range of the studies reporting a negative plant richness effect on herbivore damage (1–5 to 18–45). Therefore, the number of plant species involved is unlikely to be the reason for the direction of the diversity effect. Mechanistically, species diversity is thought to hamper herbivore foraging efficiency by diluting the resources (Root 1973), which makes the host-species harder to find. Non-host-plants can interfere with the herbivores visually (Floater & Zalucki 2000; Dulaurent et al. 2012) or chemically (McNair et al. 2000; Jactel et al. 2011).

The hypotheses supported by a general increase of herbivore damage along the tree species richness gradient are i) the Dietary Mixing Hypothesis (Bernays et al. 1994), because the increase may be a consequence of herbivores taking advantage of a diversified diet, and ii) the More Individuals Hypothesis (Wright 1983; Srivastava & Lawton 1998), because the biomass of our study plot was positively related to plant species diversity (Baruffol et al. 2013). On the other hand, the iii) Enemy hypothesis (Wright 1983; Srivastava & Lawton 1998) and the dilution effect (the iv) Resource Concentration Hypothesis (Root 1973)) would predict the opposite pattern and hence are not supported as general forces ruling the herbivory patterns in our species-rich subtropical forest. However, despite the positive relation between tree species richness and plot total leaf biomass (Pearson correlation = 0.69, $p < 0.001$), our results did not support the ii) because the total leaf biomass was not related with total herbivore damage. However, since our study reports relative damages, plots with a higher leaf biomass had likely a higher absolute biomass loss. Therefore, our results do not completely exclude the predictions of the More Individuals Hypothesis. Similar patterns with similar causes were also reported by Loranger et al. (2013).

Given the strong correlation between phylogenetic diversity and tree species richness (Person correlation = 0.96)) it was unlikely to find different results between their relations

with herbivore damages. The models showed that PD and SR were equivalent in predicting total herbivore damage. However, there was an interesting interaction between tree species richness and phylogenetic diversity (Fig. 4) showing that the positive effect of tree species richness on total herbivory damage depended on the level of phylogenetic diversity. Herbivory increased along the tree species richness gradient only if the tree species were taxonomically close, i.e. at low phylogenetic diversity. At high phylogenetic diversity changes of species richness did not affect herbivory. Consequently, our results support the idea that high tree species richness hampers the herbivores foraging efficiency when the other tree species would not be suitable, i.e. because they are very different form the primary host (dilution effect). Bertheau et al. (2010) showed a strong decrease in herbivore fitness with increasing phylogenetic distance between the original host and the new one. In contrast, additional similar tree species could be beneficial for herbivores (Dietary Mixture Hypothesis). Positive and complementary effects of diet mixing on the fitness of some generalist herbivore arthropods have been demonstrated earlier (Pfisterer et al. 2003; Unsicker et al. 2008; Unsicker et al. 2010). Our results match with findings of Dinnage (2013) and Castagneyrol et al. (2014) and underline the importance of both species richness and phylogenetic diversity in predicting herbivore impacts. Independently of phylogenetic diversity, at low tree species richness, the proportion of conspecific trees is higher and their average distance to conspecific individuals is lower than if the number of tree species is higher. Therefore, the phylogenetic diversity likely interacts with the plant species richness by modulating the number of suitable host species (phylogenetic diversity) and how much these are diluted (tree species richness).

*Differences in herbivory damage among tree species and among feeding guilds*

In order to get additional insights about mechanisms that link tree species richness (or phylogenetic diversity) to herbivore damage we now compare herbivory inflicted by the different feeding guilds investigated.

The resource dilution is likely a central phenomenon in explaining how tree species richness and phylogenetic diversity influence herbivores and the resulting leaf damage. Because a part of the herbivore species can be expected to be relatively specialized, and hence found only on some tree species, differences in herbivory damage among tree species are expected. Furthermore, these specialized herbivores should be sensible to the dilution of their resources and therefore, an effect of the relative tree species leaf biomass can also be expected. Indeed, the different tree species investigated did suffer different levels of herbivore damage (see Fig. 5 and Table 6) and were impacted differentially by the different feeding guilds (see Fig. 6 and Table 7). Additionally, we found a small but significant effect of tree species relative leaf biomass (dilution effect) on total herbivory which varied among the feeding guilds. Furthermore, the different feeding guilds were also differently affected by tree species richness or phylogenetic diversity. Altogether, these results point towards differences in feeding guild degree of specialization and therefore to different reactions to tree species richness and phylogenetic diversity among feeding guilds (Novotny et al. 2010). However, the interaction of tree species richness with phylogenetic diversity that we observed for the total herbivory damage was not influencing differentially the different feeding guilds. Nevertheless, because chewers were possibly to a greater extent generalist (Novotny et al. 2010), the increasing chewing damage along the tree species gradient might be the result of better plot quality for the generalist herbivores: they would profit from the diversity and complementarity of resources (Bernays et al. 1994; Unsicker et al. 2008;

Dinnage 2013; Schuldt et al. 2014). In contrast, sap-feeder damage showed a less pronounced response to tree species richness. Sap-feeding arthropods have a high degree of specialization and of host specificity (Novotny et al. 2010, referred as “leaf suckers” in this paper). Indeed, the herbivory profiles (see Fig. 6) show great discrepancies in sap-feeder damage levels among the tree species. Proportionally, the sap-feeders had the biggest relative differences. Such patterns match with a strong host selection and active avoidance of less suitable plant species. The tree species *Daphniphyllum oldhamii* was predicted to have near zero sap-feeder damage whereas *Castanopsis eyrei* was predicted to have sap-feeder damage around 3%. Therefore, because of such high host specificity, it is likely that the sap-feeders did not take advantage of the high number of plant species. Moreover, herbivore arthropods fitness has been shown to be reduced with increasing host taxonomic distance (Bertheau et al. 2010). Other studies including sap-feeders reported week plant species richness influence (Koricheva et al. 2000; Unsicker et al. 2006; Vehviläinen et al. 2007). It is worth noting that, and despite its level of specialization, the sap-feeding guild did not show the negative response to tree species richness although that would have been expected as negative consequence of resources dilution. We hypothesize that this could be a result of the tree crown size, where a single tree individual provides much more foliar biomass than smaller individuals do in younger forest ecosystems or grasslands. Hence, it is possible that the resources provided by a single tree crown could feed numerous generations of sap-feeders, thus reducing their need to search for new hosts.

Although the effect of tree species identity and the effect of phylogenetic diversity prove that herbivores are sensible to some plant characteristics, as related plant species share traits and are more similar than unrelated species (Gilbert et al. 2012; Srivastava et al. 2012), SLA and leaf toughness were not retained in any of our final models. Yet, we cannot exclude

that these leaf traits were important factors determining herbivore preferences *among* tree species because in our study, we tested these two leaf traits at the within species level (i.e. the species mean differences were first removed by fitting the species identity term before the leaf traits measured on individual branches). Our results indicate that the variation of these two traits within tree species did not explain variations of herbivore damage within tree species. Additionally, Schuldt et al. (2012) showed that leaf toughness and SLA were not important when explaining herbivore damage among tree species on tree saplings in the same study plots. Different studies additionally found that single chemical secondary metabolites were not good predictors of herbivory levels either (Carmona et al. 2011; Schuldt et al. 2012). Carmona et al. (2011) rather suggest that the particular mixture of defense traits could be the major herbivory determinant. Multivariate trait similarity has been shown to be a good proxy for herbivore damage (Pearse & Hipp 2009). But because several studies were not able to relate this defense trait similarity to phylogenetic relatedness (for ex. Agrawal & Fishbein (2006) or Pearse & Hipp (2009)), it is possible to deduce that phylogeny is linked with other non-measured traits that promote herbivores to feed on taxonomically close host species (Pearse & Hipp 2009).

*Implications of herbivory for plant diversity–ecosystem functioning relationships*

Increasing herbivory damage along the tree species richness gradient and differences in herbivory damage levels among tree species might have consequences on ecosystem functions and tree species coexistence in species-rich forests. The levels of herbivory reported in our study can already negatively impact plant fitness (Zvereva et al. 2012).

The dilution of the resources is likely to be a part of the mechanism although our results are in opposition with the Resource Concentration Hypothesis (Root 1973): tree species with

greater foliar biomass in our study plots suffered less total herbivory than species with low foliar biomass. Although in opposition with common expectations (Schuldt et al. 2010; Castagneyrol et al. 2013), Plath et al. (2011) reported an increase in specialist herbivore damage on tree seedlings that were more diluted because specialized herbivores tended to accumulate on them. The mean herbivory damage measured in our study is unlikely to cause tree mortality as other studies reported higher levels of herbivory without increased mortality (Tong et al. 2003; Plath et al. 2011; Zvereva et al. 2012). Nevertheless, the herbivory level that we report could still play a major role in shaping the tree community. This could happen because herbivory can reduce the number or the viability of seeds produced (Marquis 1988; Smith & Hough-Goldstein 2014) and can reduce plant growth (Zvereva et al. 2012; Kim et al. 2013), which in turn may reduce plant competitive abilities to reach additional resources. However, it is worth underlining that tree species relative biomass explained only a small part of the total variation in herbivore damage and thus cannot be the dominating force ruling this ecosystem. Manipulative experiments in grasslands proved that herbivory could promote plant species richness and/or evenness (Mulder et al. 1999; Stein et al. 2010). In forests, a manipulative experiment showed that arthropod herbivory could modify the tree species composition by altering seedling recruitment (Bagchi et al. 2014). These causal relationships are strong indications that the increased herbivory along the plant species richness gradient was not only a result but might also have been a driving force in maintaining tree species richness in our studied forest. In addition to the total herbivory pattern, the different feeding guild damage on the different tree species (see Fig. 6) indicates that tree species had to face different selective pressure. Furthermore, the significant interaction between the relative leaf biomass and the type of damage indicates that the feeding guild herbivore damages were sensible to the relative leaf

biomass. Such an effect may have been more important than the total herbivory damage in shaping the tree community. For instance, we hypothesize that the dilution effect might have stronger consequences on the tree fitness by changing the herbivory damage done by the different feeding guilds rather than changing the amount of total damage. For example, this can happen if specialized-arthropods accumulate on under-represented tree species. Furthermore, particular plant traits might affect only a particular herbivore feeding guild: "leaf-chewing insects are directly influenced by leaf mechanical properties and chemistry whereas sap-sucking insects are mostly affected by sap nutrient content" (Neves et al. (2010)). As a consequence, for example, an increased exposition to sap-suckers could have important consequences on plant fitness as these have been shown to be important vectors of diseases (Nault & Ammar 1989).

**Conclusion**

Our results about the relationship between tree diversity and herbivory are in agreement with the mixed importance of tree species richness and phylogenetic diversity observed by Dinnage (2013) and Castagneyrol et al. (2014) and highlight the fact that tree species richness and phylogenetic diversity have also an effect in the tree canopy of a tree species-rich subtropical forest. In addition, our results support that differences between specialist and generalist herbivores must be considered when studying effects of tree species richness on herbivory (Jactel & Brockerhoff 2007). We also showed that, even when tree species richness was in the last position of model 3, it remained significant. Such a result underlines an effect of tree species richness that is independent of differences in stand age, of tree

species-specific herbivory levels and of differences in branch height. Additionally, tree species composition was not linked with levels of damage. This further confirms that tree species richness had likely a direct effect on different herbivore groups and on the resulting herbivory. The fact that trees with less relative leaf biomass suffered from higher herbivory agrees with a dilution effect although in the opposite direction than commonly expected. This accumulation of herbivory damage, likely performed by specialized herbivores, on poorly represented tree species could be one of the mechanisms explaining the increased herbivory damage along the tree species richness gradient.

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**Tables**

Table 1. Variables overview

| **Short name** | **Definition** |
|---|---|
| Date | Sampling date |
| SR | Species richness: number of tree species with stem > 10 DBH present in the plot |
| Age | Stand age |
| Lf_bio | Total leaf biomass of the trees with DBH > 10 cm in the plot (kg) |
| Con | Contrast between the coniferous *Pinus massoniana* and the other eight broadleaved species |
| Spec | Identity of the nine most common species (or 8 if Con is applied before Spec in statistical models) |
| SLA | Specific leaf area of the tree species within the plot ($cm^2/gr$) |
| Tough | Leaf toughness of the tree species within the plot. |
| Rel_lf | Relative percentage of leaf biomass of a species within a plot |
| Height | Height (m) at which the sampled branch was located |
| Feed | Identity of herbivore feeding guild responsible for the damage (chewers, skeletonizers, sap-feeders, undefined) |
| PD | Tree phylogenetic diversity of tree species with stem > 10 DBH present in the plot |

Table 2. Variable hierarchy: the level at which the different explanatory variables were measured (the dependent variable leaf damage was measured separately on each branch for each feeding guild; this level is here called “Damage”).

| **Plot** | **Species** | **Species within plot = population** | **Individual (only random term)** | **Branch** | **Damage** | **Models** |
|---|---|---|---|---|---|---|
| Date | | | | | | 1, 2, 3, 4 |
| Age & SR | | | | | | 1, 2, 3, 4 |
| Leaf biomass | | | | | | 1, 2 |
| PD | | | | | | 1,2 |
| | Coniferous or not | | | | | 3, 4 |
| | Species | | | | | 3, 4 |
| | | Specific leaf area | | | | 3, 4 |
| | | Toughness | | | | 3, 4 |
| | | Relative leaf biomass | | | | 3, 4 |
| | | | | Height | | 1, 2, 3, 4 |
| | | | | | Feeding guild | 2, 4 |

Note: “individual” is the tree individual. There is no associated variable but it is mentioned because it is always part of the random model.

Table 3. ANOVA table of model 1. The two last lines show the results of tree species richness and stand age when their position was reversed in the model. The dependent variable was log-transformed total herbivory. For variable names, see Table 1.

| | *df* | *den df* | *F* | *P* | Direction of effect |
|---|---|---|---|---|---|
| Date | 1 | 21.1 | 4.84 | 0.039 | Positive |
| Age | 1 | 21.9 | 2.17 | 0.155 | None |
| SR | 1 | 21.1 | 12.02 | 0.002 | Positive |
| Age×SR | 1 | 21.2 | 5.19 | 0.033 | Stronger richness effect at younger stand stages |
| Height | 1 | 1036 | 23.25 | < 0.001 | Negative |
| Stand age/tree species richness reversed | | | | | |
| SR | 1 | 21.6 | 12.90 | 0.002 | Positive |
| Age | 1 | 21.4 | 1.29 | 0.269 | None |

Note: df: degree of freedom, den df: denominator degree of freedom, F: F-value, P: p-value.

Table 4. ANOVA table of model 2. Model 2b is equal to model 2a but with the tree species richness and stand age term order inverted. The dependent variable was log-transformed herbivory damage caused by the different feeding guilds. For further explanations, see Table 1.

| model 2a | *df* | *den df* | *F* | *P* | model 2b | *P* |
|---|---|---|---|---|---|---|
| Date | 1 | 21.2 | 15.44 | <0.001 | Date | <0.001 |
| Age | 1 | 21.8 | 1.64 | 0.2134 | SR | 0.0067 |
| SR | 1 | 21.1 | 8.09 | 0.0097 | Age | 0.3865 |
| Age×SR | 1 | 21.2 | 2.86 | 0.1056 | SR×Age | 0.1056 |
| Height | 1 | 965.6 | 15.73 | <0.001 | Height | <0.001 |
| Feed | 3 | 67.7 | 202.9 | <0.001 | Feed | <0.001 |
| Age×Feed | 3 | 69.1 | 7.72 | <0.001 | SR×Feed | <0.001 |
| SR×Feed | 3 | 67 | 4.08 | 0.0101 | Age×Feed | 0.0899 |
| Age×SR×Feed | 3 | 67.3 | 4.02 | 0.0108 | Age×SR×Feed | 0.0108 |
| Height×Feed | 3 | 2886.4 | 20.07 | <0.001 | Height×Feed | <0.001 |

Note: df: degree of freedom, den df: denominator degree of freedom, F: F-value, P: p-value.

Table 5. ANOVA table model 3. The dependent variable was log-transformed total herbivory. For further explanation see Table 1.

| | *df* | *den df* | *F* | *P* | Direction of effect |
|---|---|---|---|---|---|
| Date | 1 | 17.7 | 10.7 | 0.004 | Positive |
| Age | 1 | 19.5 | 1.1 | 0.314 | None |
| SR | 1 | 17.4 | 21.0 | <0.001 | Positive |
| Age×SR | 1 | 19.8 | 9.3 | 0.006 | Stronger richness effect at younger stand stages |
| Con | 1 | 70.0 | 88.0 | <0.001 | Coniferous were lower |
| Spec | 7 | 87.5 | 15.3 | <0.001 | Species were different |
| SR×Con | 1 | 80.8 | 0.5 | 0.481 | None |
| SR×Spec | 7 | 94.2 | 1.8 | 0.098 | None |
| Height | 1 | 808.4 | 11.8 | <0.001 | Negative |

Note: df: degree of freedom, den df: denominator degree of freedom, F: F-value, P: p-value.

Table 6. ANOVA table of the four interactions of interest of model 4. The other terms are not shown for the sake of simplicity. The dependent variable was log-transformed total herbivory. For further explanations, see table 1.

| | *df* | *den df* | *F* | *P* | Direction |
|---|---|---|---|---|---|
| Feed×Con | 3 | 220.0 | 126.8 | <0.001 | Different feeding guild damages for coniferous compared to the other tree species |
| Feed×Spec | 21 | 247.8 | 19.3 | <0.001 | Different feeding guild damages among broadleaf species |
| SR×Feed×Con | 3 | 230.3 | 5.0 | 0.002 | Feeding guild damages are different along the tree species richness gradient on coniferous compared to the other species |
| SR×Feed×Spec | 28 | 298.7 | 0.99 | 0.484 | Feeding guild damages are not different along the tree species richness gradient among the broadleaf species |

Note: df: degree of freedom, den df: denominator degree of freedom, F: F-value, P: p-value.

**Figures**

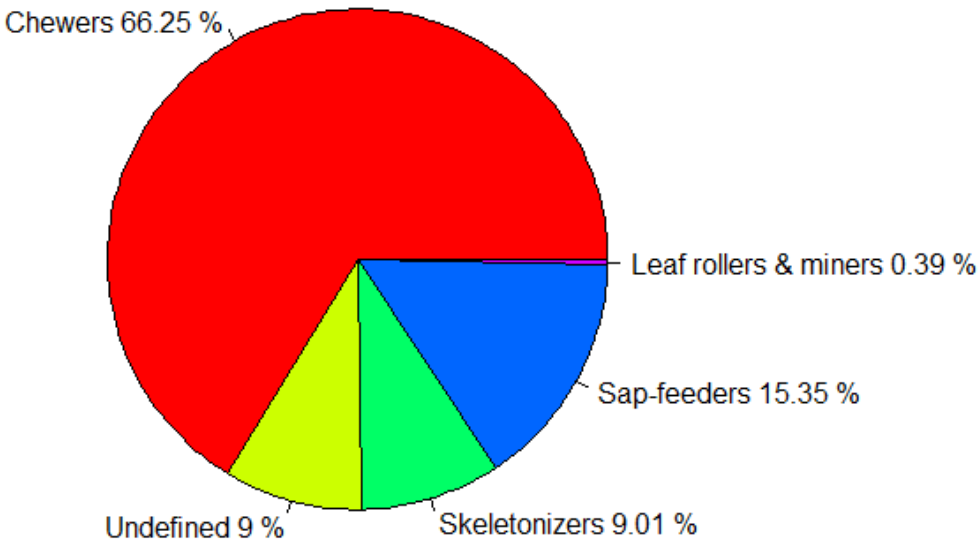


Fig. 1. Feeding guild contribution to the total herbivory damage based on plot-level averages.

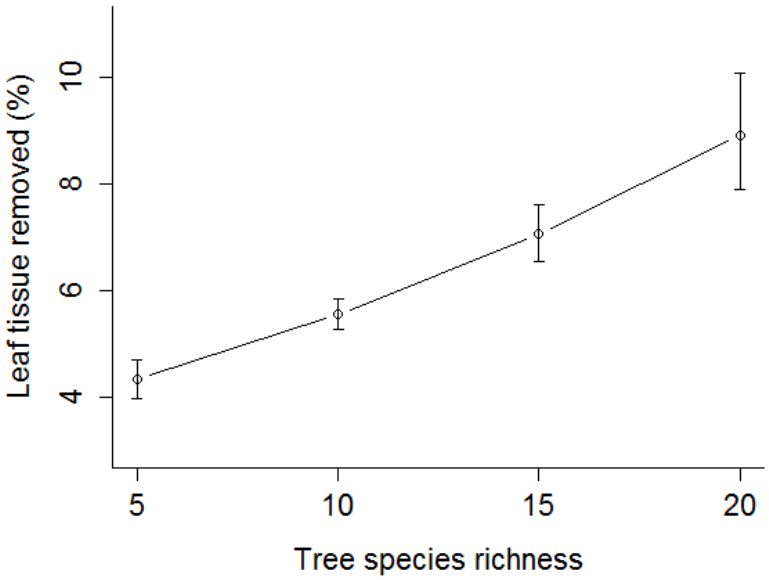


Fig. 2. Percentage of photosynthetic leaf tissue removed by herbivores (± SE) predicted by model 1 (Table 3). Predictions were calculated for the different levels of species richness by keeping the other explanatory variables at their average value. Means and standard errors are back-transformed from log-transformed percentages.

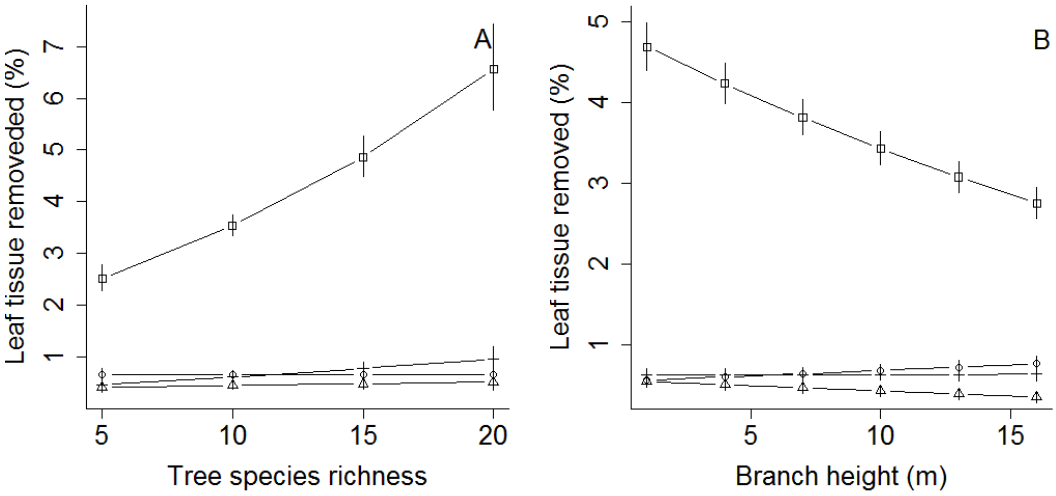


Fig. 3. Percentage of photosynthetic leaf tissue removed by the different feeding guilds (± SE) predicted by model 2b in relation with (A), tree species richness and (B), branch height. Predictions were calculated keeping the other explanatory variables at their average value. Square symbols are for chewer damage, circles for leaves damaged by undefined feeding guilds, triangles for skeletonizer damage and crosses for sap-feeder damage. Means and standard errors are back-transformed from log-transformed percentages.

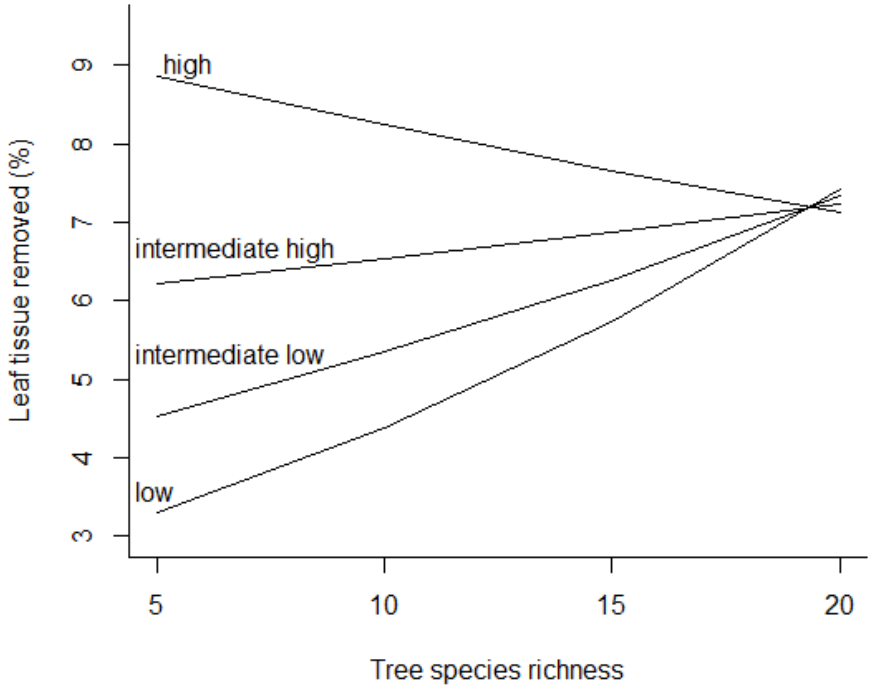


Fig. 4. Percentage of photosynthetic leaf tissue removed by herbivores predicted by model 1 along the tree species richness gradient for four level of phylogenetic diversity: “high” correspond to the most phylogenetically diverse plot value and low to the least phylogenetically diverse plot value. Predicted means and standard errors are not shown for the sake of readability.

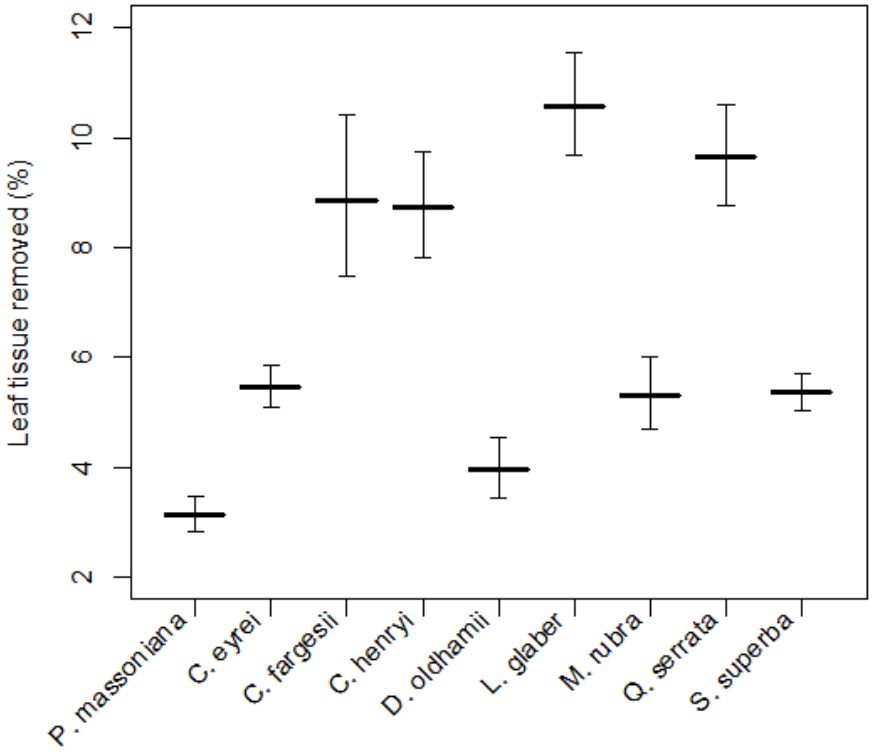


Fig. 5. Percentage of photosynthetic leaf tissue removed by herbivores predicted by model 3 (± SE). Predictions were calculated by keeping the other explanatory variables at their average value. Means and standard errors are back-transformed from log-transformed percentages.

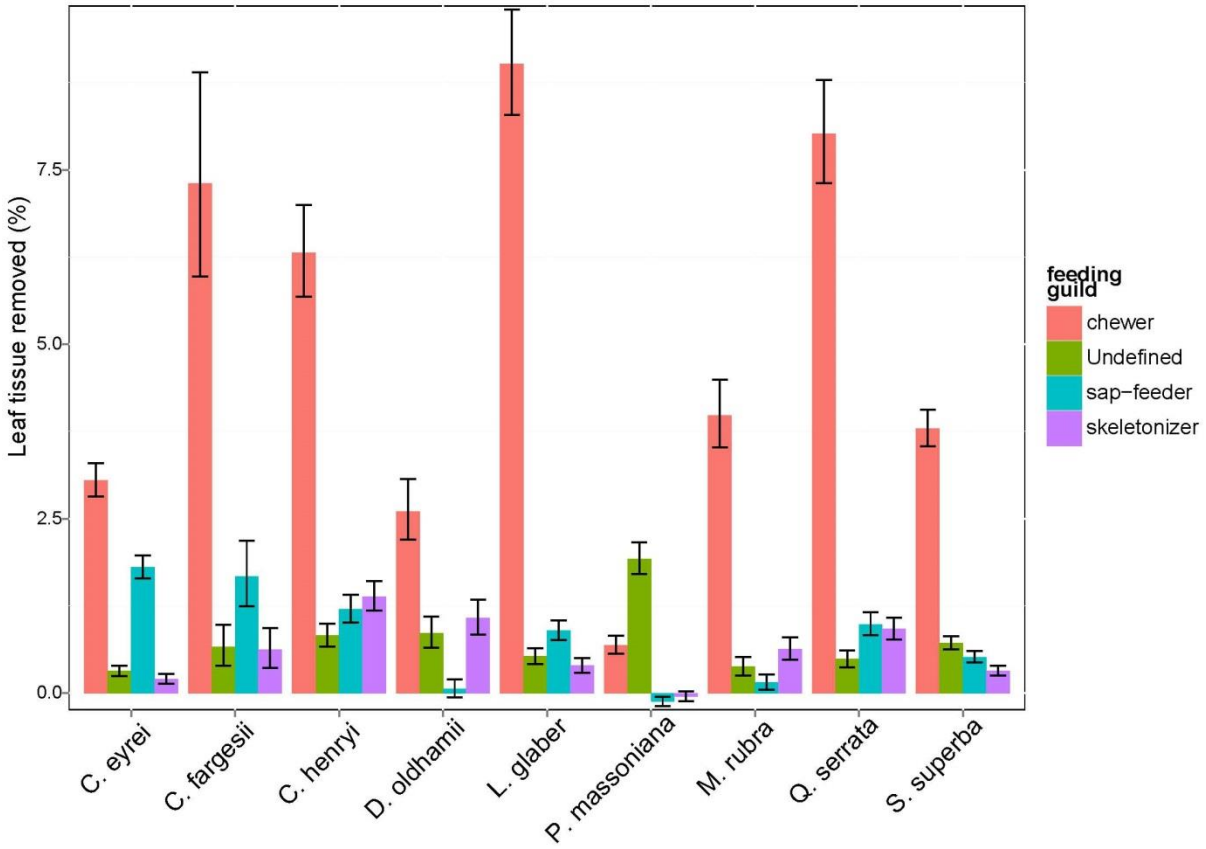


Fig.6. Percentage of leaf tissue removed (± SE) by the different feeding guilds predicted by model 4 for the different tree species. Predictions were calculated by keeping the other explanatory variables at their average value. Means and standard errors are back-transformed from log-transformed percentages.

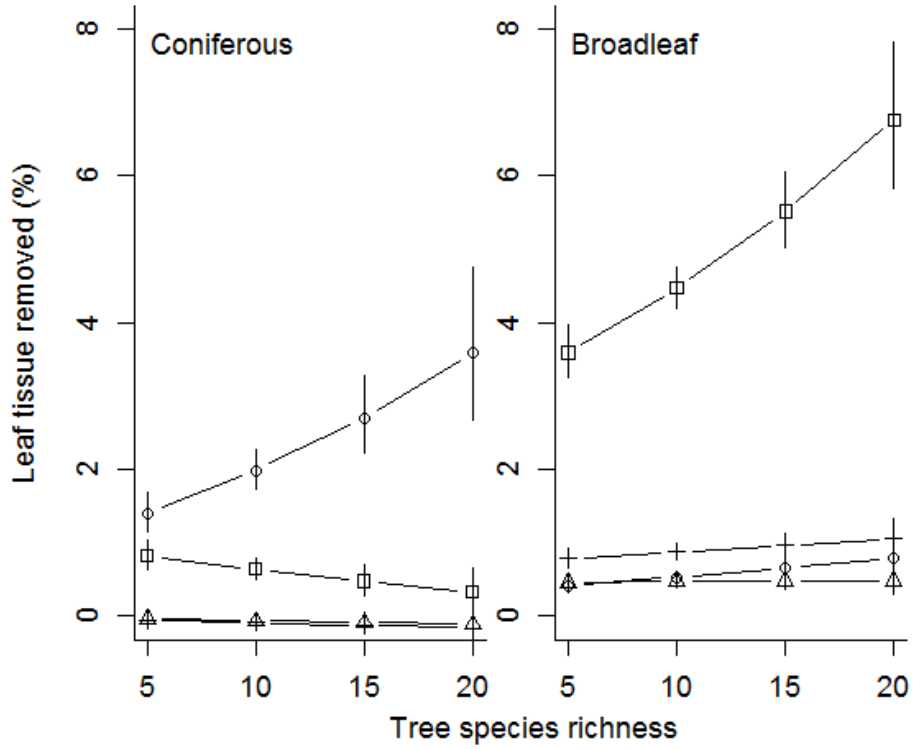


Fig.7. Percentage of photosynthetic leaf tissue removed by the different feeding guilds predicted by model 4 (± SE) for the coniferous tree species and the eight broadleaf tree species. Predictions were calculated by keeping the other explanatory variables at their average value. Square symbols are for chewer damage, circles for leaves damaged by undefined feeding guilds, triangles for skeletonizer damage and crosses for sap-feeder damage. Means and standard errors are back-transformed from log-transformed percentages.

# CHAPTER 2

# Arthropod food web structure is in accordance with bottom-up hypotheses in a plant species-rich forest in South-East Asia

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# Arthropod food web structure is in accordance with bottom-up hypotheses in a plant species-rich forest in South-East Asia

**Abstract**

*Although the importance of arthropods for ecosystem functioning is recognized, relatively little is known about factors that influence their abundance, diversity, and community composition. Different hypotheses of increasing complexity have been proposed, but regarding forests, the results remain controversial. Furthermore, the tree crown is hard to sample, resulting in even poorer knowledge of this specific habitat.*

*In order to test which of the popular hypotheses are most likely regulating the arthropod populations in a plant-species rich subtropical forest in China, we sampled arthropods within the tree crown and at 2 meters from the ground in 27 plots varying in plant species richness and in stand age.*

*Arthropod abundance increased with plant species richness and arthropod species composition depended on stand age. This increase in arthropod abundance was not related to an increase in arthropod species richness. Therefore, the total arthropod population was likely driven by the More Individuals Hypothesis. This hypothesis postulates that more energy in the system increases the number of organisms.*

*Once separated into feeding guilds, the abundances and species richness of herbivore, predator, and pollinator arthropods were neither related to plant species richness nor to plant species composition. Opposed to top-down control predictions, plant-feeding guild abundances (herbivore, pollinator and detritivore) were positively related to the predator abundance. The species composition of plant-feeding guilds was also not related to plant species composition, which excluded different hypotheses requiring arthropod niche specialization.*

*In contrast, predatory arthropods were tightly linked to their potential prey, both in abundance and in species composition. These positive relationships supported the Resource Specialization Hypothesis, the Niche Hypothesis, and the More Individuals Hypothesis as important mechanisms regulating predatory arthropod populations.*

*Although demonstrated in species-poor studies, our study contributes to accumulating evidence against top-down control of arthropod populations in species-rich forests. Our study also provides insights on arthropod abundances in the understudied canopy layer of such forests.*

**Introduction**

Worldwide, arthropods are recognized as essential actors in most terrestrial ecosystems, playing key roles in litter decomposition (Brussaard 1997), nutrient transfer (Seastedt & Crossley 1984; Belovsky & Slade 2000), or pollination (Axelrod 1960). Through herbivory and as vectors of diseases, arthropods put pressure on plants, which has implications for the promotion and conservation of plant biodiversity and ecosystem functioning (Wills et al.

1997; Mulder et al. 1999; Whiles & Charlton 2006; Bagchi et al. 2014; Fricke et al. 2014). Despite their importance, many uncertainties remain concerning the ecological controls of arthropod abundances and community structure. In part, this is because of the difficulty to study the subject (Barker & Pinard 2001) and in part because of the complexity and the variability of responses (Tews et al. 2004; Joern & Laws 2013).

Different abiotic and biotic factors can have strong influences on arthropod populations. Major abiotic factors are: past and present climate (Hewitt 2000), land history or land use (Haddad et al. 2000), and habitat connectivity or fragmentation (Kruess & Tscharntke 1994; Diekötter et al. 2008; Ockinger et al. 2010), while some of the main biotic factors are: plant species richness or plant functional richness (Haddad et al. 2009), plant species composition (Schaffers et al. 2008), resource availability (Wright 1983; Evans et al. 2005), trophic-level connectivity (Albrecht et al. 2007), and disturbances (Buddle et al. 2006).

There has been an increasing complexity of hypotheses linking plants and arthropods into a biodiversity–ecosystem functioning (BEF) framework. First, it has been suggested that plant diversity should positively affect animal diversity (Hutchinson, 1959; Southwood, 1978) and second it has been proposed that animals in turn can maintain plant diversity (Hairston et al. 1960). Then, additional hypotheses about detailed mechanisms concerning abundance and species richness of arthropods, for example the enemy hypothesis or the niche hypothesis (see Fig. 1), have been proposed. Later on, Hunter & Price (1992) suggested that the links among trophic levels can result in positive or negative feedback, i.e. the situation of one trophic level affecting its neighboring trophic level which in turn affects it back. Finally, other hypotheses relying on trophic connectivity and trophic cascades have been proposed (Eveleigh et al. 2007).

Most of the popular hypotheses linking plant diversity and arthropod communities in the area of BEF are summarized in Fig 1. One issue that still feeds the debate among researchers arises from opposite patterns predicted by some of these hypotheses (e.g. the niche hypothesis predicts more herbivores with increasing plant diversity whereas the enemy hypothesis predict the opposite situation due to a better control of herbivores by predators). Such confusion is further enhanced by publications with opposite conclusions (for example see Siemann et al. (1998) vs. Schuldt et al. (2011)). Moreover, although arthropod species richness is relatively well documented in forest canopies (Erwin 1982; Allison et al. 1993; Lowman & Wittman 1996), their community patterns linked with ecological factors such as biodiversity have been little studied in forest habitats (Basset 2003; Basset et al. 2012).

Many forest ecosystems nowadays experience the influences of anthropogenic disturbances (Hannah et al. 1994; Hansen et al. 2010). Current research tends to show that lowering ecosystem disturbances or increasing plant diversity influences arthropods in a similar manner (Albrecht et al. 2007). Young forests are expected to have a lower arthropod species richness because of their low diversity and low heterogeneity of plant resources, although evidence for this is not so clear and differs among taxa (Schowalter 1995; Burkhalter et al. 2013; Driessen et al. 2013; Joern & Laws 2013). Plant species diversity effects on arthropod diversity are further likely to become stronger with increasing stand age (Albrecht et al. 2007; Albrecht et al. 2010; Allan et al. 2013), possibly because plant species complementarity increases with time (Cardinale et al. 2007).

As higher trophic levels are more sensitive to disturbances (Petchey et al. 1999; Duffy 2003), early successional stages could have simpler arthropod communities (Albrecht et al. 2010), which in turn could affect BEF relationships. For instance, a lower number of predators per

herbivore could decrease the top-down control of herbivores and then, in turn, increase plant damage (reviewed by Schmitz et al. 2000). Also, successional stages can have direct impacts on plant diversity, biomass and species composition (for examples see Guariguata & Ostertag (2001), Meng et al. (2011), Kalaba et al. (2013)), thus, creating an additional indirect path of influence on arthropod communities.

There is a need to test if knowledge gathered from experiments can be applied to natural ecosystems and particularly to systems that are highly diverse, such as (sub)tropical forests, and where trophic interactions are considered to play a particularly important role (Cardinale et al. 2011). Most of the hypotheses shown in Table 1 have been developed for species-poor forests or grasslands (e.g. Andow (1991), Vehviläinen et al. (2008), Castagneyrol et al. 2013)), or in short-term experiments (e.g. Root (1973), Knops et al. (1999), Mulder et al. (1999)), thus potentially leading to biased estimations of general plant diversity effects on arthropod communities in species-rich natural systems. Therefore, we extensively sampled and quantified arthropods with commercially available yellow sticky traps in the forest canopy and understory of a species-rich subtropical forest in South-east China. The forest stands used in our study ranged in age from less than 20 to more than 80 years. Shrub and tree species richness ranged from 25 to 69 species per plot of 900 square meters. We related arthropod abundance and diversity patterns to this plant species richness range to investigate which of the different BEF hypotheses (Fig. 1) were supported. The forest successional stages were included in the analysis to test if plant species richness effects on arthropod communities were altered by stand age. Stand age, referred to as successional stage, was used by Bruelheide et al. (2011) as the main factor explaining variation in variables such as plant height or plant biomass in these study plots. Here we focus on plant species richness as the main factor explaining arthropod patterns. Although

our study plots were chosen in a way that plant species richness and successional stage were factorially crossed as far as possible, this was not fully realized and thus a separation of their effects was not completely possible. Nevertheless, our design made sure we had a good spread of richness and age levels, defining it as a "*comparative study"* rather than a sample survey according to Snedecor & Cochran (1989). Comparative studies have a better power to detect effects of explanatory factors than sample surveys do. Our study plots are referred to as "CSPs" for *Comparative Study Plots*.

In a previous study of the same plots, Schuldt et al. (2011) analyzed ground-dwelling arthropods and found a negative link between plant diversity and predator epigeic spider diversity and abundances. Additionally, there was an increase in leaf damage by herbivores on woody plant saplings with increasing plant species richness (Schuldt et al. 2010). These results speak against a top-down control of herbivores by predators (enemy hypothesis) and enhance the doubt raised by Riihimäki et al. (2005) and Zhang and Adams (2011) about its importance in forest ecosystems. However, the plant-species richness effects could be different in the canopy, where a great amount of resources and numerous consumers are situated (Basset et al. 2003) and where the majority of the energy assimilation takes place (Lowman 2009). Moreover, the assessment of the plausibility of some hypotheses linking predators to plant diversity requires information about the primary consumer level. This is because, for an equally high abundance of predators, it would be possible to find a low abundance of herbivores, thus indicating a top-down control, or a high abundance of herbivores, rather indicating a bottom-up control. Hence, we collected all kind of arthropods and separated them into feeding guilds in order to reveal relationships between them.

To test which of the hypotheses depicted in Fig. 1 were supported in our Chinese forest, we asked the following questions: i) are arthropod abundances, species richness, or species composition related to plant species richness? ii) Do abundances, species richness, or species composition differ between predatory arthropods and plant-consumer arthropods? iii) Is the relation predators–plant-consumers different from the relation plant richness–predators or plant richness–plant-consumers?

**Materials & Methods**

*Experimental Design*

We established a comparative study in 2008 in the Gutianshan National Nature Reserve (GNNR) in Kaihua County, Zheijiang Province, China (29°8’18’’-29°17’29’’ N, 118°2’14’’-118°11’12” E). The local topography consists of narrow valleys and forest-covered mountains ranging from 250 m to 1260 m above sea level. The forest type is a warm-temperate laurophyllous forest, described as subtropical in the literature. The majority of the tree species are evergreen and broad-leaved (Yu et al. 2001).The rainfalls occur mainly from March to September, with a yearly amount of ca. 2000 mm. The average annual temperature is 15.3°C (Yu et al. 2001).

The GNNR was established in 1975 in order to protect the old evergreen broad-leaved forest. The area contains 57% natural secondary forest up to 180 years old. Starting about 80 years ago the forest was disturbed by agriculture and charcoal production (Legendre et al. 2009). These disturbances (mainly clear-cutting but also selective harvesting) were not temporally evenly distributed within the reserve, which resulted in the presence of different

successional stages (also referred to as “stand age”). A total of 27 plots of 30 x 30 m (measured on the ground, i.e. not corrected for slope) were marked in the field to represent different levels of plant species richness and stand age, as far as possible in a factorially-crossed way. Stand age was assessed by coring the largest individuals and by additional knowledge about the last logging events (Bruelheide et al. 2011), and in 2010 the plots were divided into five age categories. The number of plots per category was 5 for stand age < 20 yr, 4 for < 40 yr, 5 for < 60 yr, 6 for < 80 yr and 7 > 80 yr. Nine plots had less than 38 woody plant species, nine plots had between 38 and 44 species and nine plots had more than 44 species. Each plot was subdivided into nine subplots of 10 x 10 m.

*Arthropod sampling*

Data collection took place from the end of June to mid-August 2010. Ten yellow sticky traps used for pest control in gardens (9 x 11 cm sticky area, double face, MIOPLANT, Switzerland) were placed in each study plot. The plot understory layer was sampled by setting 5 traps at 2 m height fixed on top of bamboo sticks. One bamboo trap was positioned in the center of the plot, the four others in the center of the four corner subplots. The sticky sides of the bamboo traps were oriented East-West. The plot canopy layer was sampled with the other five traps hung in the crown of five tree individuals (hereafter called the “tree traps”) selected to approximate the tree species composition of the plot. To do so, individuals belonging to the five most abundant tree species with stems >10 cm diameter at breast height (DBH) were chosen within each plot. Summed area at breast height was used to discriminate between two equally abundant species. Whenever less than five tree species were present, the most abundant species was used twice. Within tree species, individuals were chosen at random. Tree traps were positioned to be inside the tree crowns whenever

possible. Their height ranged from 3 m to 18 m above the ground, while the tree canopy heights ranged from 7 m to 30 m. Fishing wire (diameter of 0.35 mm) passing over the branches situated in the upper part of the canopy was used to hang the traps while a small ballast fixed on the opposite trap extremity was used to stabilize them. The traps were exposed for 6–9 days depending on the plot. This irregular exposure time was a consequence of logistic difficulties to visit the plots. After collection, the traps were protected by a plastic film and stored in a freezer until further processing.

*Yellow sticky trap sampling considerations*

Yellow sticky traps, as colored interception traps, necessarily induce a bias in the kind and in the amount of arthropod sampled: flying adults are much more likely to be trapped than sessile or juvenile individuals (Missa et al. 2008). Additionally, the color itself induces a bias toward the arthropod species that are specifically attracted to yellow. But according to Hoback et al. (1999), trap color does not affect the number of arthropod species captured. Arthropod abundances are trap-type dependent and are therefore unreliable for total arthropod estimation (Johnson 1950). However, the goal of our study was to compare sites: since the same sampling bias was present in each plot, the comparison remained meaningful. Missa et al. (2008) showed that the type of habitat had much more influence over the arthropods sampled than did the catching method.

*Insect sorting and counting*

Arthropods were identified directly on the traps and were classified by order, part of them further by families and then, based on external morphological characteristics, by morphospecies. Larvae were considered as separate morphospecies because their diet often

differs from their respective adult form (e.g. Lepidopteran, folivore larvae but nectarivores adults). In total, 37 morphospecies were recognized as larvae and 561 as adults. Based on the taxonomical knowledge of one of us (JZ) and the inspection of the arthropod mouthparts, each morphospecies was assigned to one feeding guild: folivores, sap-suckers, predators (including parasitoids), detritivores, pollinators (as adult butterflies which do not damage leaves anymore) and miscellaneous herbivore arthropods that could not be classified more precisely (mostly thrips and different fly species).

*Data analysis*

Sap-feeder, folivore and miscellaneous herbivore arthropods were aggregated into a new single feeding guild, the herbivores. They are hereafter only considered as such. They are defined as arthropods consuming above-ground living plant tissues and that have a negative impact on plants (in opposition to nectarivores that were assigned to the pollinator feeding guild). The other feeding guilds were considered separately.

Because plots were selected to represent different levels of plant richness and successional stages, we were primarily testing these effects and avoided the use of plot covariates such as altitude, exposition or total plant basal area which might have increased explanatory power but at the expense of reduced parsimony. With only n=27 plots, parsimony was prioritized in order to avoid overfitting and multiple testing issues. For all analyses at the sub-plot level, CSP-identity or its interaction with fixed-effects terms were used as random-effects terms. This ensured that plot-level terms were tested against residual variation among CSPs as error. Any plot-level covariates were thus included in this error, potentially making tests of plant richness and successional stage too conservative.

All analyses were run in R (Core Team R Development 2012) using internal functions and some special purpose R packages (see below). The analyses including several replicates within CSPs were done using generalized linear mixed models run with ASReml for R (Gilmour et al. 2009). Pearson's correlations at the plot level between all the feeding guilds and the plant species richness were calculated to quantify the relations among them. These correlations included individual abundances, species richness and rarefied species richness.

All the models illustrated below started with two covariates: the collection date and the trap exposure duration; their effects were therefore controlled. Additionally, the models contained the two explanatory terms woody plant species richness and stand age, and their interaction. Although not significant (Pearson's $r$ = 0.30, n = 27, $P$ = 0.13), plant species richness and stand age share a non-negligible amount of information. In order to reveal any potential combined or antagonist effect, the models including those two terms were run twice exchanging the positions of these two explanatory factors.

The total and the separated feeding guild abundances were investigated using generalized linear mixed models with a Poisson distribution. The type of trap and interactions of it were tested against the interactions between the type of trap and CSP-identity. The different species richness measures of arthropods (total and separated feeding guilds) could not be tested in the same way as the abundances. Since one morphospecies can be present on more than one trap within a plot, summing the morphospecies per trap would lead to an overestimation of the plot value. We therefore only counted the unique species by adding up trap values to get a pooled total per plot. Arthropod total species richness and abundance were correlated (Pearson's $r$ = 0.58; $P$< 0.01; n=27). Thus, we also calculated a rarefied species richness using the least abundant plot as reference (n=500 arthropod individuals per plot) with the R package "Rich" (Rossi 2013)). The same strategy was applied

to the separate feeding guilds. However, the detritivores feeding guild could not be rarefied because its abundance was null in one plot. It is important to note that this correction for abundance is not necessary per se as it is in sample surveys where different sampling efforts are compared (Gotelli & Collwell 2001). In our case, the same area of trap was exposed in each plot, albeit for different time intervals. Thus, total species richness remained an interesting response variable in our analyses. Linear models were used to analyze the effect ofof stand age and plant species richness levels on the different feeding guild species richnesses and their rarefied equivalents. Inspection of residuals indicated that no data transformation was necessary.

*Multivariate analysis*

To assess links between plant species richness or stand age and the total arthropod species composition or the species composition of the different feeding guilds, Nonmetric Multidimensional Scaling (NMDS, calculated with the package "vegan" for R (Oksanen et al. 2012)) was used. The collection date and the time traps were exposed in the field were as well included as explanatory variables. The morphospecies recognized as "larvae" were removed from the analysis in order to compare a genuine species composition. NMDS has the advantage that it does not rely on a particular distribution of the data and is not affected by extreme values; it is considered as a robust unconstrained ordination technique in community ecology (Oksanen 2006). The analysis was done in two steps: first, a two-dimensions ordination was done with the function "metaMDS" of the vegan package, which is optimized to best ordinate the plots. The Jaccard dissimilarity index was used to calculate the distance among plots. Second, the explanatory terms (collection date, trap time exposure, plant species richness and stand age) were fitted in turn. The variables were

oriented in the direction of their most rapid change and of their highest correlation in the ordination space. The variables were permuted randomly $10^4$ times to calculate an empiric p-value (Oksanen et al. 2012).

To further investigate if the different species compositions of the different trophic levels were linked among them or among feeding guilds, we tested their species distance matrix among the 27 CSPs for correlations. A distance matrix consists of a measure of dissimilarities between all possible plot pairs. A regular correlation cannot be calculed because the distance pairs are not independent (Smouse et al. 1986). The correlation test was done with a Mantel test (package "ade4"; (Dray et al. 2007)) which takes into account the non-independences of the distance pairs and additionally builds an empiric p-value using a random permutation procedure ($n=10^4$). A plant distance matrix was included to investigate if the plant species composition was correlated with the arthropod species composition. The plant species distance matrix among the 27 study plots was calculated using all woody plant species with individuals above 3 cm in DBH.

**Results**

*Distribution of arthropods by order and by feeding guilds*

In total, 28'198 arthropods belonging to 18 different orders and 598 morphospecies were trapped. By order, arthropods were divided as follow (number of individuals; number of morphospecies): Acari (148; 12), Araneae (347; 64), Blattodea (2; 1), Coleoptera (380; 42), Collembola (5122; 21), Dermaptera (1; 1), Diptera (12'515; 99), Ephemeroptera (2; 1), Hemiptera (200; 17), Homoptera (5'564; 192), Hymenoptera (2272; 54), Isoptera (10; 2),

Lepidoptera (253; 33), Mecoptera (1; 1), Odonata (2; 2), Orthoptera (178; 23), Phasmatodea (8; 5), Thysanoptera (1193; 28). By feeding guild, the arthropods were divided as follow (number of individuals; number of morphospecies): detritivores (5'286; 38), folivores (230; 43), miscellaneous (4'889; 65), pollinators (9'987; 150), predators (2'044; 94) and sap-suckers (5762; 208). Folivores, sap-suckers and miscellaneous herbivores grouped as "herbivores" totalized 10'881 individuals and 316 morphospecies.

Plot-identity fitted as factor in a linear model explained 32.5% of arthropod abundance variability and 68.6% of arthropod species richness variability among traps (Fig. 2). On average, there were 105.1 (± 8.0, SE) arthropod individuals trapped on the bamboo traps and 89.8 (± 5.7, SE) individuals on the tree traps, which was significantly lower ($F_{1,238}$ = 6.78, $P$<0.01). However, the average number of arthropod morphospecies on the bamboo traps (26.1 ± 1.7, SE) was not significantly different ($F_{1,238}$ = 0.21, $P$>0.05) from the number of morphospecies captured on the tree traps (26.4 ± 0.7, SE, Fig. 3).

*Feeding guild correlations and environmental effects*

No arthropod feeding guild was correlated in abundance or in species richness with the plant species richness (Table 1). The abundances of herbivores and detritivores were positively correlated with the predator abundance whereas the abundance of pollinators was not. Similarly, the species richness of predators correlated with the species richness of herbivores and of detritivores, but not with the pollinator species richness (Table 1, Fig. 4). Using the rarefied species richness, none of the former significant correlations remained, which indicates that they were at least in part abundance mediated (Table 1). Predator, herbivore, detritivore, and pollinator species compositions were all correlated among each other, showing that the species were not assembled at random (Table 1).

The mixed models revealed only small effects of environmental variables. Although total arthropod abundance was significantly related to plant species richness if stand age was first taken in account, this relationship could be observed only for the detritivores when feeding guilds were analyzed separately (Table 2). Herbivores were found in greater abundance on the tree traps. The opposite was true for the detritivores and the predators (Table 2). Predator but not herbivore abundance was related to stand age through an interaction with trap type: predators tended to become more abundant on bamboo traps and less abundant on tree traps along the stand-age gradient, and this independently of plant species richness (Table 2, Fig. 5).

Total arthropod species richness was not influenced by stand age or by plant species richness. Herbivore and predator species richness were only influenced by the collection date, the pollinators additionally by stand age and the detritivores only by the time the trap was in the field (Table 3). Besides a positive relationship between the collection date and the rarefied herbivore species number, no effect was observed on the rarefied species numbers of any of the feeding guilds (results no shown).

The total arthropod species composition was strongly affected by the collection date (Table 4, Fig. 6)). A similar result was obtained for herbivore and pollinator species compositions whereas the detritivores and the predators showed a different pattern (Table 4). Only when the different feeding guilds were considered together a relationship with stand age was observable (Table4). The species composition of the different feeding guilds was not related to stand age or plant species richness.

**Discussion**

The number of studies that investigated factors influencing arthropod communities in tree species-rich forest canopies remains low and therefore limits our ability to make inferences on important mechanisms occurring there (Barker & Pinard 2001). Our study is consistent with a general bottom-up hypothesis, although the herbivore feeding guild did not show the direct link with plant species richness predicted by most of the more specific bottom-up hypotheses (Scherber et al. 2010). These predict that the primary consumer trophic level directly depends on the amount (H n°5) or on the quality (H n°3, 4, 6) of the resources. Nevertheless, our results are in agreement with those of other studies that questioned the importance of a top-down control in forest ecosystems, in particular in species-rich and long-established warm-temperate forests (Riihimäki et al. 2005; Schuldt et al. 2011; Zhang & Adams 2011).

Total abundance, but not total species richness (i.e. not rarefied) of arthropods was related to plant species richness. An increase in abundance that is not mediated by an increase in species richness supports the More Individuals Hypothesis as general pattern at our study site. Nevertheless, the correlation between abundance and species richness of arthropods (Pearson's $r$ = 0.58; $P$< 0.01; n=27) shows that they were closely related. The Resource Specialization Hypothesis (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998), the Stability Hypothesis (Hutchinson 1959) and the Niche Hypothesis (MacArthur 1972) predicting an increase in arthropod species richness due to increasing plant species richness were not supported by our overall arthropod data. Those hypotheses are further not supported by the lack of correlation between plant and arthropod species composition,

which would have suggested species-by-species relation among producers and consumers and thus resource specialization.

Analyzed separately, only the detritivore feeding guild showed a significant increase in abundance along the plant species richness gradient whereas the herbivore, pollinator, and predator feeding guilds only showed positive trends. A possible explanation is that the different feeding guilds responded to different factors that covary with plant species richness. For example, plant species richness increases soil organic matter (Quijas et al. 2010), which could have been the important factor determining the increase of detritivore abundance (Sayer et al. 2010; Yoshida et al. 2013). Plant species richness of our plots was also positively linked with plant biomass (Baruffol et al. 2013), which could be an important factor concerning herbivore abundance (Haddad et al. 2001; Hawkins & Porter 2003). However, an additional analysis using the estimated total leaf biomass of our plots as covariate (results not shown) could not relate herbivore abundance to leaf biomass. Furthermore, the total arthropod abundance was negatively linked with the leaf biomass. But because increasing leaf biomass might interfere with arthropod displacements and thus bias the amount of trapped arthropods, it is difficult to draw conclusions from these results.

*Non-predators vs predators*

The non-predator arthropod feeding guilds, namely the herbivores, the pollinators and the detritivores, had their species composition linked with the species composition of the predators potentially preying on them. In addition, the detritivores and the herbivores (which together form 62% of the potential prey group) were correlated in abundance and in species richness to the predator abundance and species richness. These prey–predator

feeding-guild links suggest different hypotheses depending on the trophic level we are looking at.

*Predators*

The abundance and species richness of predators was positively related with the abundance and species richness of detritivores and herbivores (i.e. potential prey), signifying that predators were more abundant and more diverse where prey were abundant and diverse. This supports the More Individuals Hypothesis (Wright 1983; Srivastava & Lawton 1998), with more predators sustained by a greater availability of prey and the Resource Specialization Hypothesis (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998), with more prey species allowing a greater number of predator species to coexist. The significant correlations between the different non-predator guilds and the predator guild distance matrices (all $r^2$>0.31, P<0.01) further show that where a particular community of potential prey species was present, a particular group of predator species was present too. Because the predator species composition was independent of the plant species richness and plant species composition, it is likely that the predators we sampled displayed a high degree of specialization toward their prey and a relative autonomy from specific vegetal resources. Such results provide evidence for the Resource Specialization Hypothesis (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998) and the Niche Hypothesis (MacArthur 1972) because a particular set of resources (the prey species) is linked to a particular set of consumers (the predator species). The support for these hypotheses does not exclude the More Individuals Hypothesis (Wright 1983; Srivastava & Lawton 1998).

*Plant consumers*

Herbivore species composition was not associated with a particular plant species composition, rather indicating a generalism of diet of the herbivores. Such herbivore polyphagous patterns are in accordance with the literature (Novotny et al. 2002; Ribeiro et al. 2005). Novotny and Basset (2005) suggested that external feeders (in particular adult arthropods) are to a great extent generalists. The yellow sticky traps used in this study may have captured comparatively more external feeders, thus biasing our trapped prey species community toward generalism. Stronger links between species compositions than the ones found in our study would be expected by the predictions of the Resource Specialization Hypothesis (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998) and the Niche Hypothesis (MacArthur 1972). Hence, the fact that we did not find such links is more in accordance with the More Individuals Hypothesis: herbivores would not depend on the quality of the resources but rather on their amount. Although plant species richness and plant estimated biomass are related in our site (Baruffol et al. 2013), this link contains much variability and thus, it is possible that arthropods were sensitive to an increase in plant resources independently of plant species richness. However, the amount of resources really available to herbivores is difficult to quantify and we could not relate total leaf biomass to herbivore abundance. Estimations of total leaf biomass or tree basal area within plots might not properly reflect the resources the herbivores are foraging on. Studies measuring specifically the amount of resources available for herbivores together with herbivore abundance are required.

The Enemy Hypothesis predicts that top-down control of herbivores results in less abundant herbivores (or prey) with more abundant predators and with respectively more herbivore (prey) species being able to coexist (or at least with herbivore (prey) species having smaller

populations) (Root 1973). Although herbivore and detritivore species richness were correlated with the predator species richness, these correlations did not hold anymore when their species richnesses were rarefied, indicating that their correlations were at least partially abundance-mediated. This implies that those prey groups did not have the smaller populations that would have been predicted by a top-down control. Additionally, the abundance of those prey-like groups was positively related with the abundance of predators; hence, potential prey organisms were more abundant where their predators were abundant. This further indicates that these prey groups were not lowered by high predator abundance.

The pollinator feeding guild displayed some notable differences compared with the two other prey-like feeding guilds: its abundance and species richness were not correlated with the predator's equivalents (but species composition was). In addition, the pollinators had their species composition related with the collection date, their species richness related to stand age and their abundance was differentially related to plant species richness depending on forest age. Pollinators are usually very mobile arthropods that feed on flowers (e.g. bees, butterflies). Their presence in one particular place might thus be influenced by other environmental factors rather than local plant species richness and plant species composition. Different studies (Wettstein & Schmid 1999; Steffan-Dewenter et al. 2002; Fabian et al. 2014) suggest that pollinators might be sensitive to environmental factors at large scale only (landscape level). We further hypothesize that physical variables influenced by stand age, such as stand density, might affect the amount of pollinators trapped. Stand density was lower in old plots (Bruelheide et al. 2011), the pollinators might have moved more freely, resulting in being trapped more often. Pollinator abundance, species richness and species composition are influenced by flower density and availability (Potts et al. 2003;

Hegland & Boeke 2006). Such resources vary with the season and this might explain the relationship between the collection date and pollinator patterns.

Our results are consistent with the findings of Schuldt et al. (2011), which showed similar responses of predator arthropod species richness to plant species richness of the forest-floor stratum of the same study plots. The importance of a top-down control in long-established warm temperate forest is challenged, as Riihimäki et al. (2005) and Zhang & Adams (2011) pointed out. Because the tree canopy is difficult to access and even more difficult to sample, often the trapping locations of forest studies do not include the tree crowns (e.g. Vehviläinen et al. 2008; Schuldt et al. 2011). This could have important consequences for the results, as we showed that herbivores were trapped to a greater extent in the canopy whereas predators were trapped in greater abundance near to the ground. Such result lead us to question the generality of conclusions produced from data gathered from only one part of a spatially complex system such as natural forests. We also observed that the total arthropod species composition and the predator abundance were influenced by stand age, indicating that the old and young forest areas harbored different arthropod communities. Such a result, in accordance with the literature (Schowalter 1995; Buddle et al. 2006; Missa et al. 2008; Burkhalter et al. 2013, but see (Driessen et al. 2013) for opposite results), confirms that even at a local scale other factors than plant species richness have to be accounted for.

Several other studies also found weak effects of plant species richness on plant consumers (e.g. Hawkins & Porter 2003; Jetz et al. 2009; Koricheva et al. 2000; Vehviläinen et al. 2007; Neves et al. 2013). Plant diversity was found to not influence directly the abundance of herbivores but rather to covary with it; main causal factors were: topography (Hawkins &

Porter 2003), water and energy availability (Jetz et al. 2009), or plant species identity (Koricheva et al. 2000; Vehviläinen et al. 2007). What about the study presented here? The plot identity term explained 32.5% of arthropod abundance variance and 68.6% of arthropod species richness variance among traps. This means that the CSPs were different from each other and that the yellow sticky traps had the ability to capture these differences. A possible explanation for the low explanatory power of our major plant-level factors, plant species richness and stand age, could be that multiple other factors, each with individually low contribution, together shaped arthropod community patterns within the forest plots. Given the spatial scale of our study, climatic variables can be excluded. The topographic variables, altitude and exposition, were introduced in each model testing for arthropod species richness or abundance as covariates. Besides a positive effect of altitude on pollinator abundance ($F_{1,17.8}$ = 4.6, $P$>0.05), no other significant result could be detected (result not shown). It is possible that the lack of relatively consistent response to plant species richness was a consequence of the high plant species richness that was present even at the lower end of the range. For example, in a recent meta-analysis, Zhang et al. 2012 found that forest productivity was linked to diversity but this effect plateaued with tree richness ≥ 6. Another explanation could lay in the temporal variation that occurs within the ecosystem. It may be that the patterns predicted by different hypotheses are not visible at the moment of our study. For instance, a top-down control may not have been the dominating force at the moment of our snapshot in our study site. But maybe we would have observed it at the end of the summer. Some concrete illustrations have been described to date. For example, arthropod populations with abundances that corresponded to a bottom-up situation switched to a top-down configuration during the season in a salt marsh in New Jersey (Gratton & Denno 2003). The inter-annual arthropod species turnover can also be affected

by plant species diversity (Haddad et al. 2009). In this case, cumulative arthropod species richness rather than a snapshot would be necessary to reveal plant species richness effects.

**Conclusion**

This study reinforces the doubt raised by Riihimäki et al. (2005) and Zhang & Adams (2011) about the importance of top-down control in species-rich and long-established warm-temperate forests. Although the existence of a herbivore control by predators in some generally simpler systems is out of doubt (Zhang & Adams 2011), our highly complex system was more in accordance with a bottom-up control. Similar bottom-up controls were also observed in a large grassland biodiversity experiment (Scherber et al. 2010).

Our study pointed out a strong link between prey-like arthropod groups and their predators, both in their abundances and in their species compositions, but not in their species richness. In contrast, herbivore arthropod species richness and species composition were not related with plant species richness. The different models and direct correlations provided evidence for a bottom-up control of arthropod communities. Our data support the More Individuals Hypothesis as the main driving force on the herbivore arthropod community and the Resource Specialization Hypothesis and the Niche Hypothesis as the main driving force on the predator arthropod community.

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## Tables

Table 1. Correlations (Pearson, n = 27) among the different feeding guilds. Top-right, the abundances, down left the species richness, rarefied species richness and species compositions. The upper line in the cells below the main diagonal is the true species richness, the middle line is the rarefied species richness and the lower line is the arthropod composition correlations calculated with a Mantel test (see methods). Significances are marked with stars (* p<0.05, ** p<0.01, *** p<0.001). Detritivores were not rarefied because there was zero individual in one plot.

| | Plant species[a] | Total arthropod | herbivore | Predator | Detritivore | Pollinator |
|---|---|---|---|---|---|---|
| Plant species richness | | 0.35 | 0.35 | 0.22 | 0.06 | 0.35 |
| Total arthropod | 0.34<br>0.06<br>-0.07 | | 0.82*** | 0.40* | 0.70*** | 0.55** |
| Herbivore | 0.27<br>0.03<br>-0.04 | 0.93***<br>0.57**<br>----- | | 0.42* | 0.36 | 0.44* |
| Predator | 0.33<br>-0.12<br>-0.14 | 0.75***<br>0.06<br>----- | 0.62***<br>0.17<br>0.62*** | | 0.45* | -0.21 |
| Detritivore | 0.09<br>-----<br>-0.00 | 0.65***<br>-----<br>----- | 0.62***<br>-----<br>0.54*** | 0.46*<br>-----<br>0.39*** | | -0.11 |
| Pollinator | 0.23<br>0.33<br>-0.03 | 0.33<br>0.39*<br>------ | 0.07<br>-0.03<br>0.41*** | 0.05<br>0.16<br>0.31** | -0.14<br>-----<br>026** | |

a: arthropod species richnesses and rarefied species richnesses are correlated with plant species richness, arthropod species compositions are correlated with plant species composition.

Table 2. Results of the GLMM with arthropod abundances at trap level as dependent variable (n=266 Degree of freedom (*df*), denominator degree of freedom (*DF*), F-value (*F*), and direction of the effect (*D*, only shown if significant) are shown. The variables appear in the same order they were fitted in the model. Plant species richness, stand age and their interaction with trap type are shown additionally with their order inverted.

| | Total arthropod | | | | Herbivores | | | Pollinators | | | Detritivores | | | Predators | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | D | *dF* | *DF* | *F* | D | *DF* | *F* | D | *DF* | *F* | D | *DF* | *F* | D | *DF* | *F* |
| date | - | 1 | 21.5 | 1.2 | - | 21.3 | 0.1 | ↘ | 22.6 | 6.5* | ↗ | 21.4 | 14.7*** | ↗ | 20.4 | 4.7* |
| duration | - | 1 | 22.1 | 0.8 | - | 22.9 | 0.8 | - | 20.7 | 0.9 | - | 23.4 | 1.0 | - | 22.2 | 0.2 |
| Trap type | - | 1 | 24.3 | 2.5 | a | 22.1 | 44.5*** | - | 25.3 | 0.2 | b | 19.5 | 87.1*** | b | 21.3 | 5.9* |
| age | - | 1 | 20.9 | 0.5 | - | 21.1 | 0.1 | - | 21.8 | 0.2 | - | 17.3 | 2.5 | - | 19.8 | 0.0 |
| rich | ↗ | 1 | 20.7 | 5.5* | - | 20.9 | 3.1 | - | 20.1 | 2.8 | ↗ | 19.7 | 5.8* | - | 20.5 | 1.5 |
| Trap type*age | - | 1 | 24.1 | 2.4 | - | 22.5 | 0.8 | - | 26.8 | 0.0 | - | 16.4 | 2.0 | d | 19.5 | 5.2* |
| Trap type*rich | - | 1 | 23.9 | 0.9 | - | 20.3 | 1.7 | - | 22.5 | 0.6 | - | 20.3 | 0.1 | - | 24.2 | 0.3 |
| rich | - | 1 | 19.9 | 3.9 | - | 20.4 | 3.2 | - | 18.9 | 3.0 | - | 16.6 | 2.1 | - | 19.5 | 1.3 |
| age | - | 1 | 21.8 | 2.1 | - | 21.6 | 0.1 | - | 23.2 | 0.0 | ↘ | 20.6 | 6.1* | - | 20.8 | 0.2 |
| Trap type*rich | - | 1 | 22.2 | 0.1 | - | 17.5 | 0.8 | - | 19.9 | 0.6 | - | 14.9 | 0.4 | - | 19.7 | 0.2 |
| Trap type*age | - | 1 | 26.0 | 3.2 | - | 26.7 | 1.8 | - | 30.9 | 0.0 | - | 22.7 | 1.7 | d | 23.9 | 5.4* |
| age:rich | - | 1 | 19.4 | 4.2 | - | 19.9 | 1.7 | c | 20.2 | 6.5* | - | 15.1 | 2.7 | - | 19.1 | 0.8 |

Note: stars denote significance, *p<0.05, **p<0.01, ***p<0.001. Code of the direction's effect: a=abundance greater on tree traps; b=abundance greater on bamboo traps; c=abundance tends to decrease in young stands and increase in old stands along the plant richness gradient; d=abundance tends to increase on bamboo traps and decrease on tree traps along the stand age gradient, dF are shown only for total arthropods as they are the same for the separate feeding guilds

Table 3. Results of the linear model with arthropod species richness at the plot level as dependent variable (n=27). Degree of freedom (*df*), denominator degree of freedom (*DF*), F-value (*F*), and direction of the effect (*D*, only shown if significant) are shown. Variable are in the model in the same order as in the table. Plant species richness and stand age are shown additionally with their order inverted.

| | Total arthropod | | | | Herbivores | | Pollinators | | Detritivores | | Predators | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | D | *df* | *DF* | *F* | D | *F* | D | *F* | D | *F* | D | *F* |
| date | ↗ | 1 | 21 | 4.4* | ↗ | 8.0** | ↘ | 6.2* | - | 1.9 | ↗ | 12.1** |
| duration | - | 1 | 21 | 3.1 | - | 2.0 | - | 0.6 | ↗ | 4.8* | - | 1.3 |
| age | - | 1 | 21 | 0.9 | - | 0.4 | ↗ | 5.0* | - | 3.3 | - | 0.8 |
| rich | - | 1 | 21 | 3.1 | - | 2.3 | - | 0.5 | - | 1.2 | - | 3.5 |
| | | | | | | | | | | | | |
| rich | - | 1 | 21 | 3.8 | - | 2.6 | - | 1.8 | - | 0.3 | - | 4.2 |
| age | - | 1 | 21 | 0.1 | - | 0.1 | - | 3.7 | - | 4.3 | - | 0.1 |
| | | | | | | | | | | | | |
| age*rich | - | 1 | 21 | 0.4 | - | 1.5 | - | 0.1 | - | 0.2 | - | 0.2 |

Note: stars denote significance, *=<0.05, **=<0.01, ***=<0.001, dF and DF are shown only for total arthropods as they are the same for the separate feeding guilds

Table 4. Determination coefficients ($r^2$) and associated P-values (based on a permutation test of $n = 10^4$) of the explanatory variables in the two-dimensional space calculated with NMDS.

| | Total arthropod | | Herbivores | | Pollinators | | Detritivores | | Predators | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $r^2$ | *P* | $r^2$ | *P* | $r^2$ | *P* | $r^2$ | *P* | $r^2$ | *P* |
| Date | 0.50 | <.001*** | 0.45 | .001** | 0.45 | <.001*** | 0.07 | .409 | 0.13 | .198 |
| Duration | 0.15 | .136 | 0.16 | .114 | 0.05 | .549 | 0.11 | .276 | 0.00 | .981 |
| age | 0.24 | .029* | 0.09 | .303 | 0.13 | .175 | 0.00 | .970 | 0.11 | .237 |
| rich | 0.02 | .763 | 0.02 | .773 | 0.02 | .944 | 0.02 | .817 | 0.13 | .178 |

## Figures

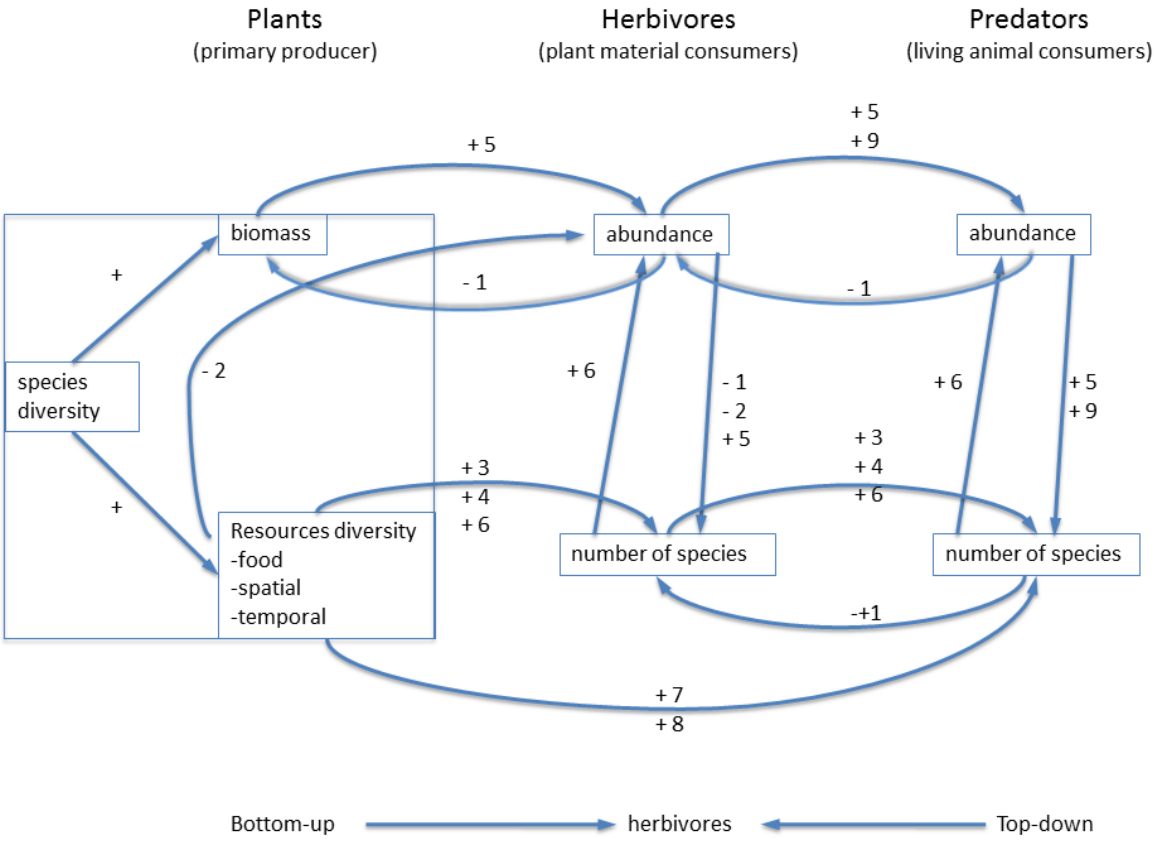


Fig. 1. Popular BEF hypotheses. The box on the left represent the explanatory variable "plant species richness" for which we cannot separate the different effects of resource diversity vs resource amount (biomass). The sign on the left of each number describes the direction of the effect.

1 Enemy hypothesis, top-down: more predator species keep the abundance of herbivores low, avoiding interspecific competition among them and hence allowing more species to coexist, in turn more herbivore species help to maintain more predator species (Paine 1969; Root 1973; Hunter & Price 1992).

2 Resource concentration hypothesis, bottom-up: the consumers are more diverse when their ressources remain diluted, there are less dominant and abundant consumer species and less pest outbreaks (Root 1973).

3 Stability hypothesis, bottom-up: greater resource diversity results in a better availability of the resources through time which prevents consumer species extinction (Hutchinson 1959).

4 Resource specialization hypothesis, bottom-up: more diverse resources allow more different specialized consumers to coexist (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998).

5 More individuals hypothesis, bottom-up: more energy in the system can support more individuals which mathematically results in more species (Wright 1983; Srivastava & Lawton 1998).

6 Niche hypothesis, bottom-up: more differentiated species can better exploit the total amount of resources and thus can be more numerous (MacArthur 1972).

7 Plant-predator dependence, bottom-up: predators directly depend on some particular plant resources (Hagen 1987), which are more available in plant-diverse habitats, e.g. for many parisitic fly species the male is nectarivore.

8 Predator habitat specialization, bottom-up: Siemann et al. (1998) suggest that several arthropod predator species can feed on one single prey species if these predators have different habitats (spatial niche separation).

9 Diversity cascade hypothesis, bottom-up: species number increases in the food web as a consequence of increasing dominant (prey) species abundance because the predators rapidely converge where the resources are (Eveleigh et al. 2007).

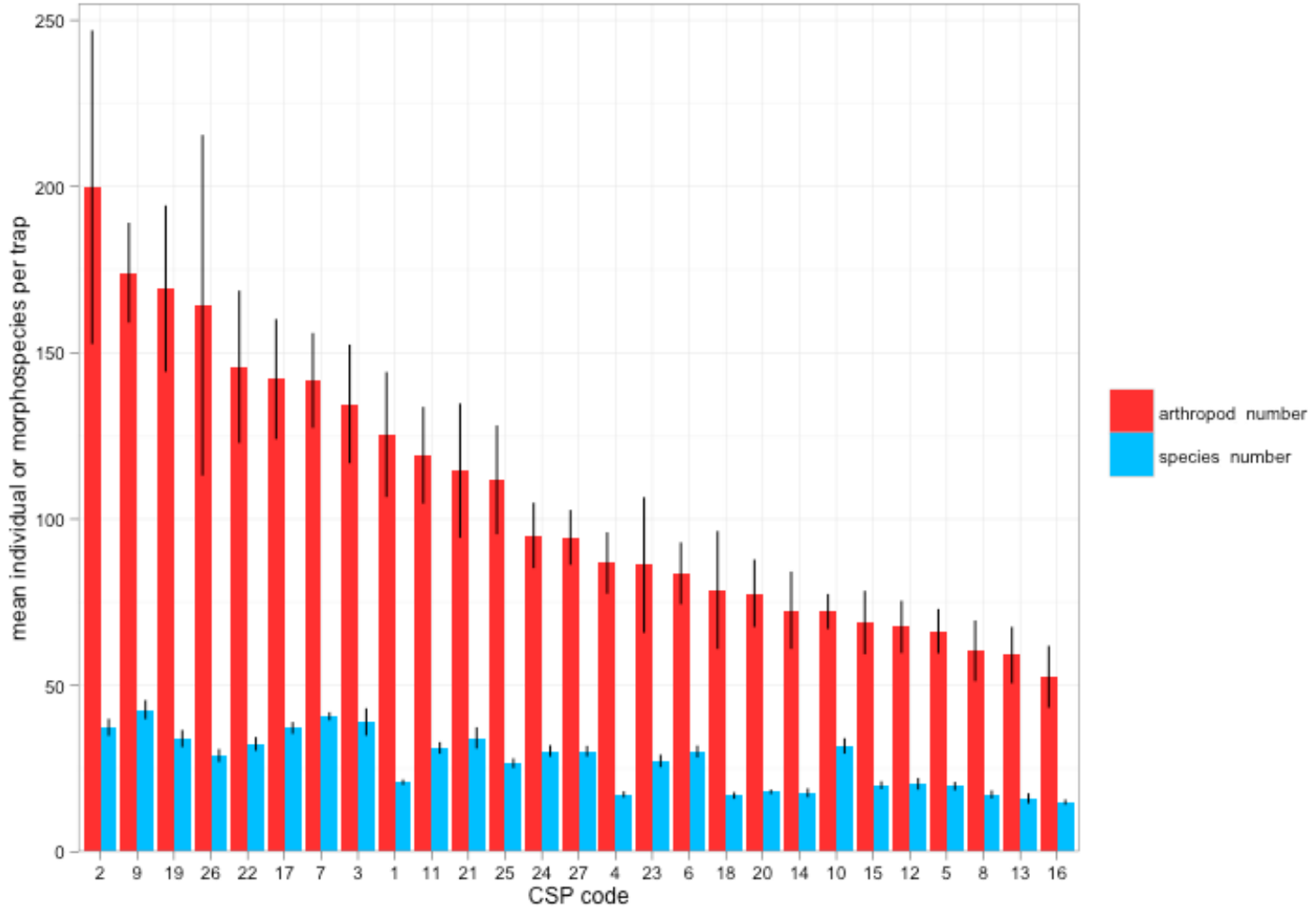


Fig. 2. Mean number of arthropods (red) and of arthropod morphospecies (blue) caught per trap in each CSP (± SEM). The CSPs are ordered in decreasing order of mean number of arthropods per trap.

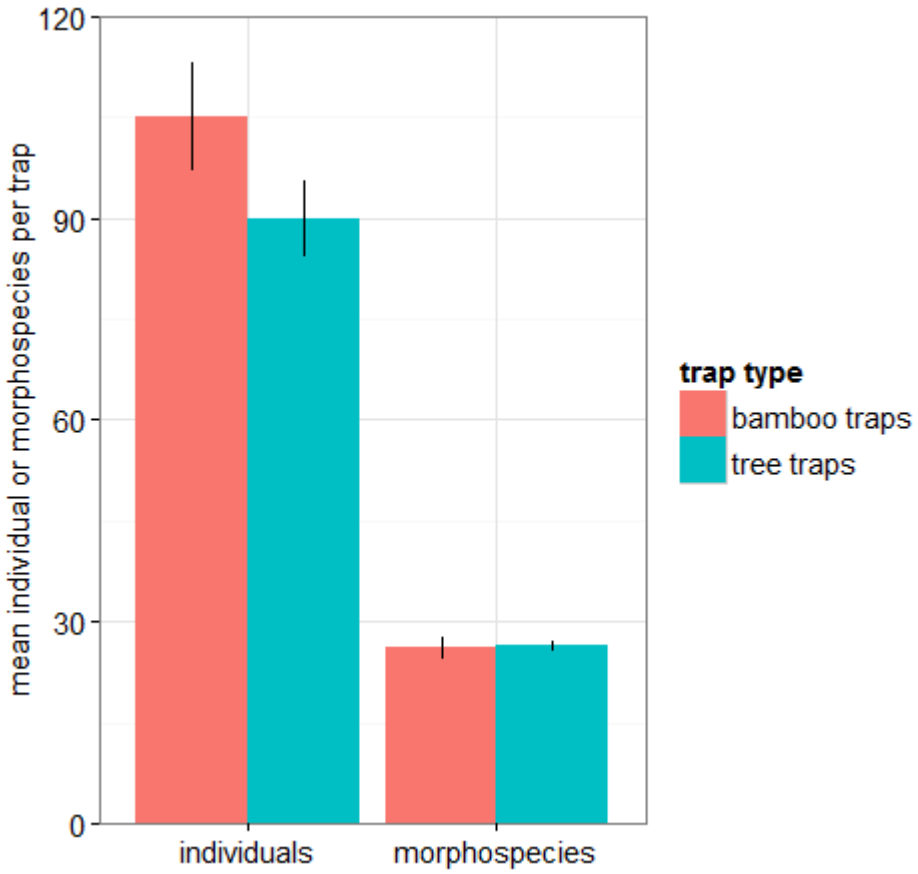


Fig. 3. Mean number of arthropod and of arthropod morphospecies caught in each trap per trap type (± SE)

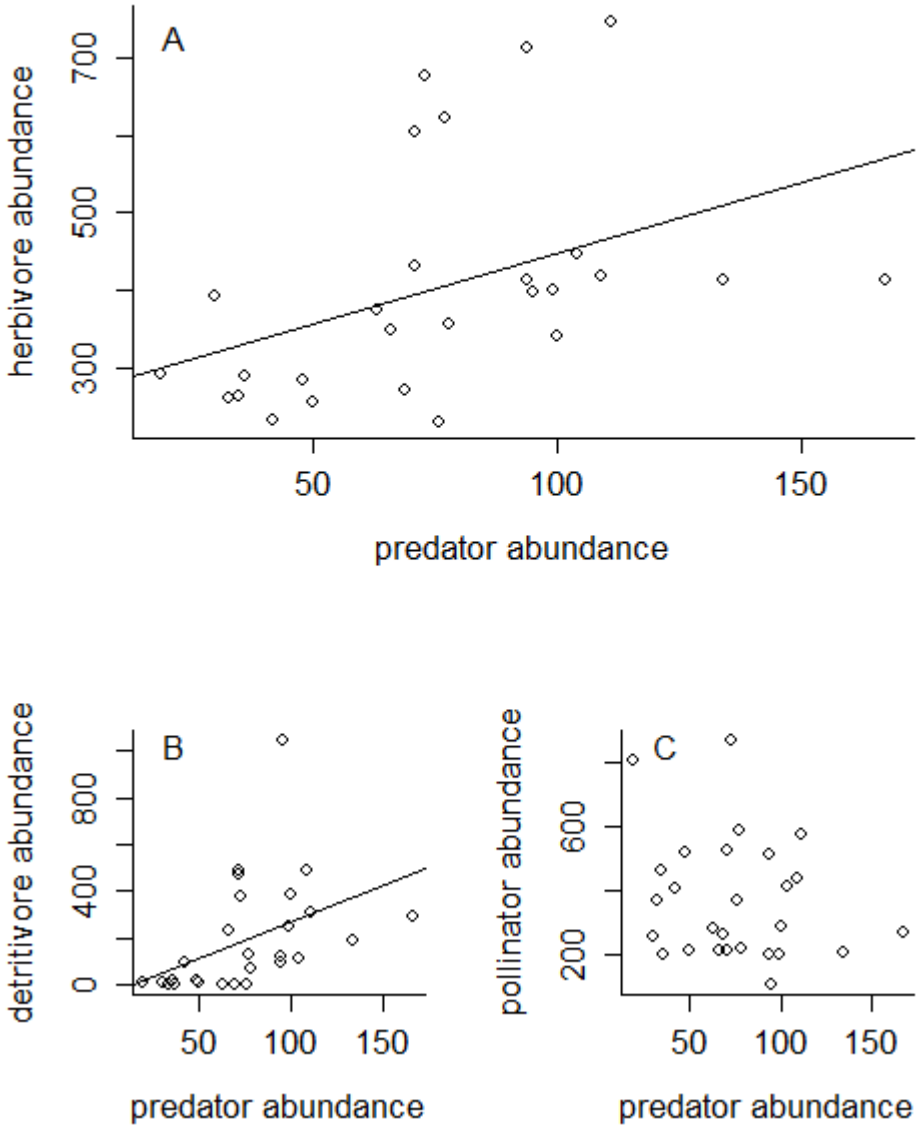


Fig. 4. Relationships at the plot level (n = 27) between (A) herbivore and predator abundance, (B) detritivore and predator abundance and (C) pollinator and predator abundance. Regression lines denote a significant correlation.

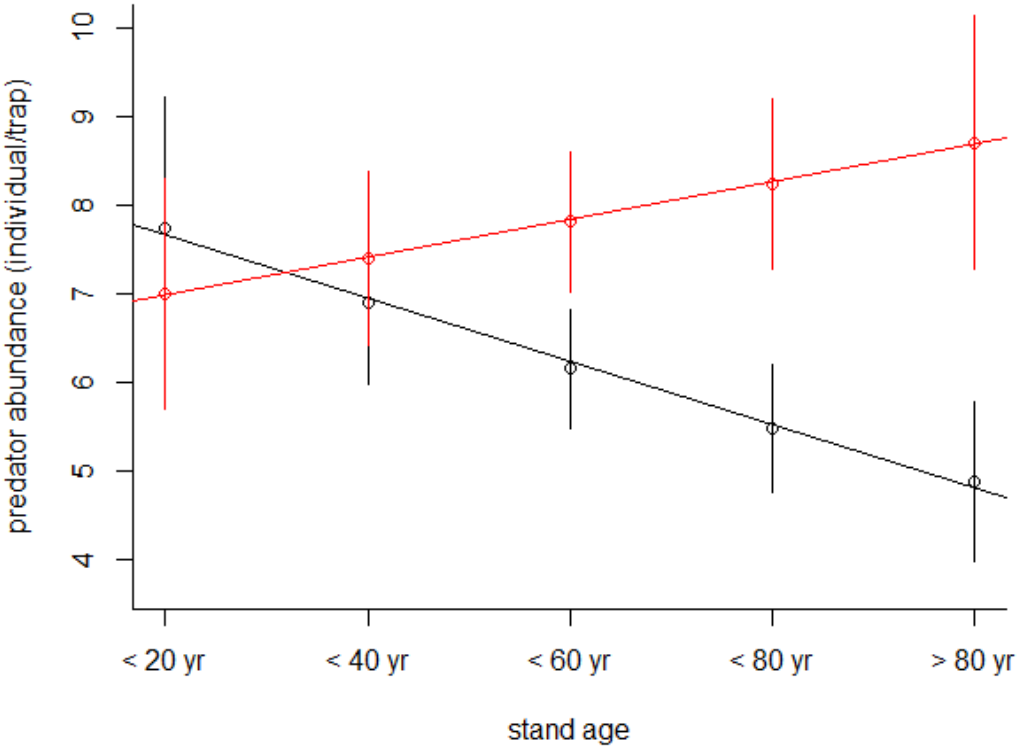


Fig. 5. Predicted predator abundance per trap (± SE) in function of stand age on bamboo (red) and on tree traps (black). Both average abundance per trap type and slope difference are significant.

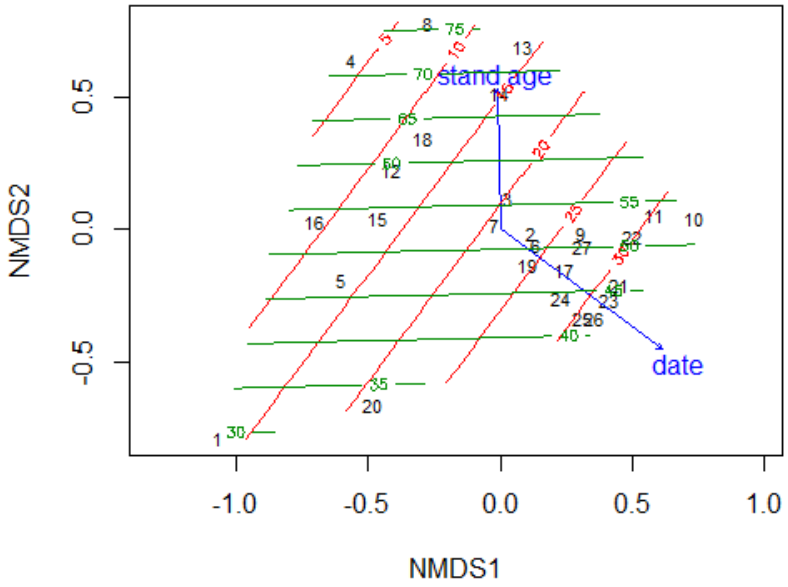


Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination in two dimensions of the 27 CSPs using the adult arthropod morphospecies (n=28'075; 561 morphospecies). Numbers in black indicate the particular plot code. Only the significant relations are shown. Arrow sizes are proportional with the correlation strength. The green lines represent the stand age gradient whereas the red lines represent the collection date gradient.

# CHAPTER 3

# Allometric equations for the total biomass and compartment biomass of eight common tree species in a sub-tropical forest in China

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# Allometric equations for the total biomass and compartment biomass of eight common tree species in a sub-tropical forest in China

**Abstract**

*In the context of climate change, the carbon cycle is of major concern. Forests are key actors in stocking, absorbing, and releasing carbon. Yet, carbon estimation methods for forests are imprecise. Elementary allometric work, i.e. building allometric equations from harvested trees, is still needed to estimate the biomass of non-harvested trees, to extrapolate to plot biomass, and to calibrate remote sensing methods. The territory of China contains vast areas of subtropical forest, yet it has been estimated with governmental allometric tables providing little detail about source data, accuracy, and applicability. Therefore, we built allometric equations for 8 common tree species found in Chinese subtropical forests. The selected species were three deciduous broadleaf species, Alniphyllum fortunei, Liquidambar formosana, and Sassafras tzumu, three evergreen broadleaf species, Castanopsis fargesii, Castanopsis sclerophylla and Schima superba, and two coniferous broadleaf species, Cunninghamia lanceolata and Pinus massoniana. In total, 154 trees ranging from 1 to 37.5 cm in diameter at breast height (DBH) were measured. Their biomasses were measured by the component compartments (leaves, branch wood, stem*

*wood, dead attached material (DAM) and roots) and as total aboveground biomass (TAB) and total biomass (TB).*

*Biomass allometric equations fitted on log-log scale explained generally more than 90% of data variability. The equation accuracies were influenced by the tree species identity or on how the species were grouped within models, on model type (linear models (LM) or mixed-effect linear models (LME) with species identity as random term), and most importantly, on the predicted biomass compartment. Species-specific models based on DBH outperformed mixed-species models, but the inclusion of wood specific gravity (WSG) as second predictor variable reduced this performance gap. Two other predictors, tree height and crown length, only marginally improved the model's predictive power. The most variable compartment was leaf biomass. The DAM compartment was excluded because of massive data heterogeneity. In summary, we recommend using species-specific models when the predictions have to be done for the same species and to use mixed-species LME models when the predictions have to be done for different (or groups containing different) species. Finally, the mixed-species LME model based only on the DBH was used to estimate forest plot biomass. Predictions quality is discussed in view of data quality and tree size range in the plots. Different sources of error are also discussed.*

**Introduction**

Awareness of climate change and its alarming consequences is increasing worldwide (O'Neil & Oppenheimer 2002; Thuiller 2007; Poloczanska et al. 2013). One crucial element of this process is atmospheric $CO_2$ concentration (IPCC 2007). Forests are recognized as playing a

key role in regulating atmospheric $CO_2$ as sink, reservoir, and source (Phillips et al. 2008; Schimel 2014). Highest authorities such as the Food and Agriculture Organization of the United Nations (FAO) or the World Meteorological Organisation (WMO) acknowledge this key role. In this context, the United Nations Framework Convention on Climate Change (UNFCCC) requires countries to report accurately and regularly their carbon stocks, meaning that correct carbon assessment methods are essential. Yet, it is still a challenge to quantify the amount of carbon stored, released or gained by forests with enough accuracy to be able to report changes occurring during relatively short time spans (2–10 years). Furthermore, remote sensing techniques are recently gaining popularity in estimating carbon stocks, but there is still an urgent need to improve their precision by calibrating these techniques with ground-based carbon estimations (Asner et al. 2010; Le Toan et al. 2011).

One of the best methods to quantify biomass at large scale is to apply allometric equations built from destructive sampling and tree-level data of forest inventories (Hall et al. 2001). These equations relate tree biomass of harvested individuals to non-destructive variables, such as diameter at breast high (DBH), tree height (H) and crown length (CL). Biomass upscaling is performed by selecting representative forest plots in which the size of every tree is inventoried and then calculating the plot biomass by applying the allometric equations to each tree. The result is expressed as biomass per area which can be extended to larger scale (Hall et al. 2001). Although carbon content has been shown to vary among tree organs or forest types (Thomas & Martin 2012), the carbon mass is traditionally estimated as being 50% of the biomass (Brown 1986). We retain this assumption for the sake of simplicity.

Various difficulties and concerns remain with regard to allometric equation construction. First, tree biomass does not only depend on DBH, tree height and crown length but also on

tree architecture and wood density. These vary among forest types, tree species, individuals, and local environmental conditions (Ketterings et al. 2001; Correia et al. 2010; Henry et al. 2010; Banin et al. 2012; Lines et al. 2012; Chave et al. 2014). Hence, including several equations from different forest types and site-specific or species-specific correction factors are likely to produce better estimations (Chave et al. 2014). Second, the measurement of tree biomass is an arduous time and resource-consuming activity, which makes it difficult to obtain sufficient data to develop precise allometric equations. Although previous studies published sets of allometric equations for tree standing biomass, often the belowground biomass was missing, and therefore the tree total biomass was not included in the equations (Ketterings et al. 2001; Chave et al. 2005; Henry et al. 2010; Chave et al. 2014). The root system is an important biomass compartment constituting on average 10–45% of the total biomass (Cairns et al. 1997; Wirth et al. 2004; Correia et al. 2010; Luo et al. 2012; Ruiz-Peinado et al. 2012). The root biomass allometric equations are often not of high quality because only a fraction of the sampled trees are really measured above and below ground (Wirth et al. 2004; Correia et al. 2010; Ruiz-Peinado et al. 2012). These few measurements are used to construct root to shoot ratios that are afterwards extended to the rest of the measured trees (e. g. Fang et al. 1998; Razakamanarivo et al. 2012).

Additionally, detailed allometric equations predicting the different tree biomass compartments are required for other areas of research such as plant physiology or ecosystem functioning ecology. In this regard, compartment allometries were used to scale-up branch-level gas exchange (Morén et al. 2000; Damesin et al. 2002), arthropod load (Hijii et al. 2001), tree growth, and carbon circulation (Levia 2008; Bascietto et al. 2012). Leaf biomass allometric equations were also used to calibrate different remote sensing methods (Running et al. 1986; Turner et al. 2005; Arias et al. 2007).

Although a substantial amount of work has been conducted in tropical forests (analysed by Chave et al. 2014), less has been achieved in sub-tropical forests (Keith et al. 2009; Henry et al. 2011). China contains large subtropical forest areas (Wu 1980) that are now under heavy anthropic pressure (Wang et al. 2007). Biomass estimations of Chinese forests exist but provide little detail about source data, accuracy and geographic and environmental applicability. Original data referred to in the literature (e.g. in Wu et al. 2014) are for example governmental tables from anonymous authors. These tables for instance contain volume data that are then converted into biomass using conversion factors (Fang et al. (1998). Additionally, these volume tables are incomplete and only coniferous species could be properly estimated (Fang et al. (1998). For more accurate predictions of biomass and carbon storage, it is urgent to establish refined methods which additionally provide error estimates.

In the context of the research platform of BEF-China (DFG FOR 891, www.bef-china.de, Bruelheide et al. 2014), we decided to build our own set of allometric equations using trees from the subtropical forest in the south of China. We derived equations for the estimation of tree total above-ground biomass (TAB), total biomass (TB) and biomass for different compartments: leaves, branch wood, stem wood, dead attached material (DAM), and roots. Our aim was to provide 1) accurate species-specific or mixed-species allometric equations including new predictors that improve estimation accuracy, 2) simpler species-specific or mixed-species allometric equations requiring less predictors because all of the variables that we measured are not always available in other surveyed forests, and 3) a concrete example of how to use these equations for calculating total biomass in forest plots of the region.

## Methods

### *Site information*

The trees were sampled in Jiangxi Province, South-East China. The region has a subtropical climate and accumulates 2000 mm of rainfall throughout the year (Yu et al. 2001). The forest has been exploited as a tree plantation with about 80% of the trees being *Cunninghamia lanceolata.* The remaining 20% of the trees were naturally present and established freely from the surrounding natural forest. The site (29°11′ N, 118°01′ E) is situated at the end of a small valley with a relatively steep slope (30 degrees on average at tree locations).

### *Materials and Measurements*

Eight species available along a reasonable range of DBH were chosen. In order to perform unbiased regressions, data are required to be regularly located along the X-axis. Therefore, we sampled one tree per centimetre of DBH up to the biggest available size. The species belong to three functional groups: coniferous, broadleaved evergreen and broadleaved deciduous (Table 1, Appendix 1, www.eFloras.org).

### *Tree biomass reconstruction*

The sampling protocol was adapted from Snowdon et al. (2002). Trees were divided into different parts: woody parts (stem and woody part of the branches with diameter equal or greater than 3 cm), twigs (branches with diameter smaller than 3 cm) and dead attached material (DAM). The root compartment was measured by another project (Li et al. 2013). In order to calculate the dry biomass, different subsamples of each biomass part were carefully

chosen to represent the whole range of possible values, hence avoiding extrapolation beyond the data range. Below are the details.

*Woody compartments*

The stem and the woody parts of the big branches were measured by segments. The volume of each segment was calculated with the truncated cone formula, equation 1:

$$V = 1/3 \times \pi \times l \times (r_1^2 + r_1 \times r_2 + r_2^2) \quad (1)$$

Where *l* is the length, $r_1$ the basal radius, and $r_2$ the apical radius of the segment.

The typical segment length was 100 cm. If the segment had irregularities, particularly nodes at side branch location, its length was shortened in order to record these size variations. Stem- and large branch-wood volume was recorded with this procedure until the threshold diameter of 3 cm was reached. Data on wood specific gravity (WSG, dry biomass per fresh volume, g $cm^{-3}$), were gathered from several wood slices that were cut from each tree. Five slices were sampled on the stem: one at each extremity and one at each quarter. A sixth slice was sampled just below the first branch (crown start). The WSG of branch segments was obtained by randomly selecting one branch per crown third and then by sampling a wood slice near the branch start and another slice near the 3 cm threshold. Wood slice positions were all recorded. The volume of the wood slices was calculated using the cylinder formula (*V=area*thickness*), where thickness is the average of four equally spaced measurements and area is the average of the two cylinder surfaces. The program "ImageJ" (http://rsbweb.nih.gov/ij/) was used to measure the slice surfaces from scanned slice images. The slice dry biomass was obtained by oven drying at 80°C to a constant weight.

*Twigs*

Twigs were defined as the apical part of the stem, the apical part of the large branches and the side branches whenever their diameter did not exceed 3 cm. Each twig's initial diameter and position were recorded. Twig dry biomass was obtained by sampling two twigs per crown third (n=6). In most of the small trees, all twigs were sampled. Twigs were randomly selected with different diameters and health conditions in order to avoid selection biases (like taking only the healthiest branches). In the laboratory, twig wood and twig leaves were weighed separately; approximately 10% of their fresh mass was re-weighed and oven-dried for two days at 80°C.

*Dead attached material (DAM)*

DAMs were either big dead branches or dead twigs. Since they were often broken, we recorded their diameter and their length. The volume of the DAM was estimated with the cone formula:

$$V = 1/3 \times \pi \times l \times r^2 \quad (2)$$

Where *l* is the length of the DAM piece measured in the field and *r* its basal radius.

Several small pieces of DAM with different diameters were randomly chosen in the field. Their fresh volume was calculated with the truncated cone formula (equation 1). The whole DAM sample was then oven-dried for two to three days at 80°C.

*Biomass reconstruction*

The biomass of each segment, twig and DAM piece measured in the field was estimated using respective models based on the wood slice, twig and DAM samples. All the models were mixed-effect species-specific models with individuals fitted as the random factor. Biomass of dry samples was considered exact, i.e. with no measurement errors. Model selection was achieved by running a leave-one-out cross validations (LOCV). Models having the highest $R^2$ and the lowest bias between predicted LOCV values and real values were chosen. The selected models were then run in a Bayesian framework (WinBUGS program, http://www.mrc-bsu.cam.ac.uk/bugs) allowing to propagate the errors by summing the different estimations within the model.

In brief, estimates were calculated from the posterior distribution drawn out of three Markov Chain Monte Carlo (MCMC) simulations. Each chain ran a total of 500'000 iterations from which the first 300'000 were discarded. Among the 200'000 valid iterations, one in twenty (n=10’000) was kept to avoid correlation between consecutive estimates. Each biomass estimate is the mean of the retained valid simulations (n=30’000) and is therefore characterised by the standard deviation of these. Compartment biomass and TAB for each tree were calculated within the model. The sums of the segments, of the twigs or of the DAMs were estimated with their own standard deviation (Appendix 1). A model run was considered successful when all parameters and estimates converged (Gelman & Hill 2007). For few estimates, such complete convergence was not reached, thus leading to proportionally bigger standard deviations. It is worth pointing out that these standard deviations are *model errors*: they characterize the simulation variability. Small trees that were entirely sampled have no model error: their standard deviation equals zero. Only non-informative priors were used, insuring the estimates to be strictly based on our data. In

order to avoid statistical redundancy, no allometric predictor variables were used in the biomass reconstruction process.

The biomass of the stem and of the large branch wood was calculated by multiplying the estimated segment WSG with the segment volume. WSG was modelled as a function of stem (branch) length, segment average area, and relative segment position within stem (branch). Leaf, wood and total twig biomass were modelled as a function of twig diameter and position in the crown. As twig biomass variability increased with its diameter, twig standard deviations were modelled as linear functions of twig diameter. DAM biomass was calculated by multiplying the volume with the estimated species-level WSGs as a few DAM samples were lost and it was impossible to assign DAM-WSG for individuals. The variability of individual estimates was used to calculate a species-specific standard deviation. TAB was calculated by re-running in parallel the models developed to calculate the twig, the DAM, and segment biomass and by summing the estimates within the model. Root data did not allow a standard error to be calculated. TB contains root biomass and therefore has no standard deviation either.

*Statistics*

A separate analysis was run for each compartment (leaf, branch wood, stem wood, dead attached material and root), for the total aboveground biomass and the total biomass for each species, functional group, or all species together. For the sake of simplicity and to avoid heteroscedasticity, the data (except WSG) were log transformed. Models containing several species were run twice: as a linear model (LM) and as a linear mixed-effect model (LME) using species as the random term. The entire original dataset can be found in Appendix 1. Although important (Peichl & Arain 2007), tree age was not included as it was not easy to

determine for species lacking clear annual growth rings. Furthermore, we aimed to construct "user friendly" equations comparable with the majority of already published equations. Hence, only the most common predictors, DBH, tree height and crown length were fitted. Additionally, tree species identity was used to obtain a WSG value at the species level from the dataset published by Zanne et al. (2009). Published WSGs at species level were preferred for two reasons. The first justification is to make the equations transposable to other individuals or species without having to make new measurements. Second we aim to avoid the statistical redundancy of using WSG to reconstruct the individual tree biomass (see above) and to estimate the allometric equations. Nevertheless, a comparison showed that our measured WSGs averaged at species level correlated well (Pearson's $r$ = 0.89, n = 8, $P$ = 0.003) with the published WSGs and had not bias. In addition, WSG has been shown not to vary systematically with tree DBH (Baker et al. 2004; Nogueira et al. 2007). Because the same predictors used in this study are not necessary measured in other studies, models of decreasing complexity were fitted in order to provide the best models depending on predictor availability. ANOVA tables, AIC values, and model fit comparisons (analysis of variance for LM models and likelihood ratio tests for LME models) were used to retain the minimal model (note: LME models were fitted with "maximum likelihood" in order to perform likelihood comparisons). Polynomial terms and interactions were deliberately not used, as they risked increasing prediction errors albeit improving model fit.

Different parameters were used to describe model quality and goodness of fit. First, the $R^2$ of the model described the amount of data variability accounted for. The $R^2$ for LME models was obtained with a special function, "lmmR2" (package "lmmfit", Maj 2011). In a few cases, the $R^2$ is not provided because LME models were fitted with ASReml for R (Gilmour et al.

2009). Second, we calculated the standard error of the residuals (RSE). This is a common goodness of fit measurement in allometric analyses and also used to correct the back-transformed results (see equation 4).

$$RSE = \sqrt{\frac{\sum Residuals^2}{Residuals\ DF}} \quad (3)$$

The back-transformed biomass values corrected for the logarithmic bias according to Sprugel (1983) were obtained using the following equation:

$$predicted\ biomass = e^{fitted\ values} \times e^{RSE^2/2} \quad (4)$$

Back-transformed prediction quality was assessed by the average deviation (AD). This relative error measurement compares how different the predicted biomasses are from the real corresponding biomasses.

$$Average\ deviation\ \% = \frac{100}{n} \sum |predicted\ biomass - real\ biomass| / real\ biomass \quad (5)$$

*Biomass scaled to plot level*

To illustrate how a model can be applied to forest plots, we used the data from 27 comparative study plots (CSP) established within the BEF-China project (www.bef-china.de, Bruelheide et al. 2011). The tree species used in our study occur naturally in these plots. The list of trees with DBH > 10 cm iss provided by Baruffol et al. (2013). The total biomass of the individual tree was predicted with the simplest mixed-species LME model. This model only scaled TB with DBH and did not use species identity to make predictions:

$$\ln TB = \alpha + \beta \times \ln DBH \quad (6)$$

Model parameters were: α= -1.73; β= 2.30, RSE= 0.204, AD= 23.7%. Equation 4 is used to back-transform the predicted values into tree individual biomass. Plot biomass is obtained by summing the individual tree biomasses. Finally, we applied the equation provided by Chave et al. (2014) to calculate the coefficient of variation at the plot level:

$$ADplot = AD \times \frac{\sqrt{\sum_t (TBest(t))_2}}{\sum_t TBest(t)} \quad (7)$$

Where *ADplot* is the average deviation of the plot, *AD* is the average deviation of the model, and *TBest* is the estimated biomass of tree *(t)*.

**Results**

*Biomass in relation to DBH*

The different biomass compartments, the total above-ground biomass, and the total biomass were exponentially related to the DBH (Fig. 2). This relationship was successfully linearized by a logarithmic transformation, which also homogenized the variance, except for the DAM compartment and to a lesser extent the leaf compartment. The DAM compartment displayed the highest variability because of large trees with a very small or a null DAM biomass, followed by the leaf compartment. Thus, the models of these two compartments were also characterized by the highest average deviation (Table 3 and 6). When the biomass

compartments were summed to obtain TAB and TB, the relation between the DBH and the biomass became very regular, with only little variability left (Table 8 and 9). The proportion of the different biomass compartments varied with DBH (Fig. 1). For example, the stem biomass was approximately three quarters of the TAB at small DBH but only two thirds at large DBH. The proportion of leaf biomass became smaller and the proportion of branch wood became larger as the DBH increased. The proportion of DAM was very small and did not produce a noticeable biomass fraction at any DBH size.

*Allometric models for different compartments (Tables 4-9)*

Model ADs revealed that LM models were in general slightly better or performed equally well as LME models. However, LM models tended to have more significant predictors than LME models. The variability these predictors could explain was accounted for by the random term in LME models (i.e. species). Whenever LM and LME models contained the same predictors, AD values were similar but with a small advantage for LME models. Although the DBH explained most of the biomass variability, the AD could be lowered by some additional predictors in some biomass compartments. Tree height and DBH were highly correlated (Fig. 3) which explains why tree height only marginally improved most of the biomass predictions.

*Leaf compartment (Table 3)*

Leaves were the second most variable biomass compartment (first being DAM). Compared with the mixed-species models, the AD was substantially lowered by grouping the species into functional groups, and to a lesser extent by fitting species-specific models. ADs remained high for several species, like *Cunninghamia lanceolata* (53.1%) and *Castanopsis sclerophylla* (45.8%). Species-specific differences concerning leaf biomass were also reflected

by the difference in predictor number between the mixed-species LM and LME final models: the LME model retained only the DBH while the LM model kept the full set of predictors. WSG was retained in several minimal models predicting leaf biomass.

*Branch wood compartment (Table 4)*

Additionally to the DBH, branch wood biomass was mostly explained by WSG in both LM and LME mixed-species models. Tree height did not play a significant role, but crown length did. Biomass prediction for *Sassafras tzumu* remained very variable even using species-specific models.

*Stem wood compartment (Table 5)*

The stem wood compartment was the least variable compartment. When WSG and tree height were included, the ADs of both LM and LME mixed-species models became very low, less than 13%. This indicates that once DBH, tree height, and WSG were accounted for, the shape of the stem was similar among species.

*Dead attached material compartment (DAM) (Table 6)*

DAM compartment was by far the most variable biomass compartment. ADs ranged from 62% (*Pinus massoniana*) to several thousand % for models grouping species and for some species-specific models as those for *Alniphyllum fortunei*, *Liquidambar formosana*, and *Castanopsis fargesii*. This was first because the DAM compartment was very variable (see Fig. 2), which impacted negatively the AD. Second, there were several large trees with a DAM biomass of zero. The predictions for those trees were characterized by massive average

deviations since there was a large difference between the biomass predicted and the real biomass.

*Root compartment (Table 7)*

The mixed-species LM model retained the whole set of predictors while only the DBH (except tree height for two species) was retained by the species-specific models. Together, these results indicate that crown length and tree height influenced the root biomass to different extent depending on the species because they reflected species-specific patterns.

*Total aboveground biomass (Table 8)*

Models predicting TAB were characterised by high $R^2$ and low ADs. The whole set of predictors was retained in both LM and LME mixed-species models. The AD of both full models was circa 15%. After the DBH, WSG was the most important predictor in both mixed-species LM and LME models. Once the effect of WSG was accounted for, only a small AD improvement could be obtained by fitting the functional groups separately. These results indicate that the relationship between DBH and tree volume was relatively constant across species.

*Total biomass (Table 9):*

TB models led to very similar results as TAB models; ADs and minimal models were similar.

*CSP total biomass prediction (Table 10)*

CSP's total biomass was predicted to range from 1018 kg (7.5% plot AD) to 29'240 kg (3.4% plot AD).The aforementioned biomass values correspond roughly to a range of half a ton to

15 tons of carbon (corresponding coarsely to 11 tons to 325 tons by hectare). The plot with the lowest biomass was a young plot of less than 20 years whereas the plot with the highest biomass was an old-growth plot of more than 80 years. Those two plots were situated at the two age extremities of the CSPs. Individual tree prediction bias is shown by the regression line in Fig. 4, trees under circa 19 cm of DBH tend to be overestimated and trees above 19 cm of DBH tend to be underestimated. The bias slope was significant ($t(152)= -2.51$, P=0.013). The overall bias of this model was 6.2 % (sd=2.63) and was significant ($t(153)=2.36$, P=0.020). Although the underestimation of the big trees could lead to an underestimation of the total plot biomass, this should not sensibly impact our estimates because only 3.7% of the trees in the plots were above 40 cm of DBH (Fig.4).

**Discussion**

*Predictor importance, biomass compartments, model quality*

It was important to have a different set of models for each biomass compartment as their proportions varied with tree size (Fig. 1). Tree ontogeny, which is closely related to tree size, is associated with varying biomass compartment proportions (Wirth et al. 2004; Peichl & Arain 2007; Shaiek et al. 2011). These varying proportions also reflect effects of tree physiological changes on biomass allocation, i.e. the woody parts increased with tree size whereas the photosynthetic part decreased.

The relative importance of the different predictors – and therefore the selected final model – depended on the tree species identity or on how the species were grouped within the model, on model type and, most importantly, on the biomass compartment. Generally, the

mixed-species models contained more significant predictors than the functional group or the single-species models, indicating that these predictors could describe species-specific characteristics. For example, crown length was an important leaf biomass predictor in the mixed-species LM model but was almost never significant in the single-species models. This underlines an interaction between species identity and crown length. In other words, a given increase in crown length resulted in different increases of leaf biomass depending on the tree species. For applications, it means that using these additional predictors in part can substitute for distinguishing among species. The predictors were also of different importance when comparing model type, especially the mixed-species minimal models: in most cases, LME models retained fewer significant predictors than the LM models. LME models included the species identity as a random term, which partially accounted for species-specific differences. For example, in the leaf biomass models the mixed-species LM retained the whole set of predictors while the equivalent LME model only retained the DBH. Hence, predictors that remained significant in mixed-species LME models have a general relationship with the biomass that held through the eight species. For example, the branch wood biomass was affected by DBH, crown length and species-specific WSG independently of the species identity.

*Leaf compartment:*

The four predictors were retained in mixed-species LM models predicting leaf biomass. While the DBH, tree height, and crown length appear reasonable predictors as they are related to the part of the tree sustaining the branches, our results also showed that WSG positively influenced leaf biomass. Within functional group, WSG positively influenced evergreen leaf biomass, negatively influenced coniferous leaf biomass, and did not influence

deciduous leaf biomass. It is, however, unclear why WSG influenced leaf biomass. Statistical redundancies can be excluded as WSG was not used to calculate the original leaf biomass. As WSG is related to wood mechanical strength (van Gelder et al. 2006), it is possible that species with high WSG could sustain higher leaf loads without breaking. On the other hand, WSG is also associated with wood hydraulic conductivity (Swenson & Enquist 2008), which could explain the pattern observed for the coniferous species. Only DBH was retained in mixed-species LME models. This indicates that crown length and tree height were mainly describing differences among species.

*DAM*

DAM data were very heterogeneous, especially because of big trees having no DAM. Therefore, predictions at individual level were unreliable. Similarly, other authors reported high uncertainties concerning DAM prediction (Wirth et al. 2004; Peichl & Arain 2007). DAMs do not follow regular allocation rules because they are not a functional part of the tree, but rather a consequence of self-thinning or structural damages. Different authors analysing the biomass by compartment did not include DAMs as separate compartment (see Wang 2006; Shaiek et al. 2011; Tabacchi et al. 2011). Since DAMs only represented a very small fraction of the total biomass (0.8%), we argue that their precise quantification is not necessary for general allometric studies, especially for predicting TAB and TB.

*Other compartments, total aboveground biomass and total biomass*

Branch wood, stem wood, root biomass, TAB and TB models were characterised by high $R^2$ and low RSEs and ADs. The best mixed-species models predicting TAB and TB accounted for a large part of data variability (97% to 99%) and had ADs (15% to 25%, depending on the

predictors used) comparable with the values reported by other authors: Nelson et al. (1999) reported ADs of 14% to 19.8% for mixed-species models, Basuki et al. (2009) reported ADs of 27% to 30%, Tabacchi et al. (2011) reported an AD of 14%, and Chave et al. (2005) reported ADs ranging from 12% to 16%. Prediction quality was better for TAB and TB than for the separate biomass compartments (except for the stem). This means that the sum of the compartments was less variable than the compartment themselves. Such a pattern was also reported in other studies (eg: Peichl & Arain 2007; Shaiek et al. 2011) and could be explained by the link between DBH and the mechanical stress the individual can tolerate (Niklas & Spatz 2004), and therefore the mass it can sustain before breaking.

Despite model differences among species, groups of species, model types or biomass compartments, WSG was often the most important biomass predictor after accounting for DBH as it increased the $R^2$ and reduced ADs and RSEs to a greater extent than the tree height or the crown length. This is likely because DBH, crown length, and tree height as geometrical descriptors are highly correlated (see for example Figure 3). Therefore, little variability concerning tree volume or shape is left once DBH effects have been taken into account. WSG is not related to DBH (Baker et al. 2004; Nogueira et al. 2007) and therefore can add important and independent information for biomass prediction. Concerning the tree species of this study, the published WSG (Zanne et al. 2009) varied from 0.32 to 0.54 (g $cm^{-3}$), resulting in a potential mass variation of 70% for a given volume. Previous studies also demonstrated the importance of WSG in predicting biomass (eg. Chave et al. 2005; Basuki et al. 2009; Henry et al. 2010; Alvarez et al. 2012; Chave et al. 2014).

*Which model should one use?*

Measuring additional predictors is labour intensive and therefore their usefulness must be assessed in advance. Tree height (and crown length which requires tree height to be calculated) is difficult to measure in closed canopies as treetops might not be visible. Species level WSG is easy to obtain because it only requires identifying the tree species.

In the case of TAB and TB, after fitting the DBH, the additional significant predictors only explained 1 to 2 percent variability. Moreover, most of AD reduction was obtained by fitting WSG. For instance, the four predictors were significant in the mixed-species LME model for TAB prediction. WSG lowered the AD by 7.4% while tree height lowered it only by 1.6% and crown length by 0.3%. Similar predictor importance was observable concerning the different biomass compartments: after accounting for DBH, predictors added relatively little model explanative power and only lowered the Ads slightly. Therefore, we advise to record tree species identity to assign a WSG value rather than measuring tree height or crown length.

Fitting species-specific or functional group models differentially improved model fits compared with mixed-species models depending on biomass compartments. Fitting improvements were particularly sensible concerning leaf biomass. ADs were on average halved in the species-specific models compared to the mixed-species models. This appears reasonable as this compartment was the most variable (except for DAM). In contrast, branch wood biomass models were only little improved by fitting species-specific models, particularly when the mixed-species models contained WSG. The species-specific models scaling the stem biomass with only the DBH performed better than the corresponding mixed-species model. But when tree height and WSG were added, the mixed-species models performed similarly to the species-specific models. Hence, these descriptors were capable of

describing species-specific differences and could be useful to make predictions as precise as possible. Contrasting with the previous biomass compartments, ADs of mixed-species root biomass models were greatly lowered for some species by fitting species-specific models (*Alniphyllum fortunei*, *Sassafras tzumu*, *Castanopsis sclerophylla*, and *Pinus massoniana*) and lowered much less for the other species (*Liquidambar formosana*, *Castanopsis fargesii*, *Schima superba* and *Cunninghamia lanceolata*). This suggests that the root biomass was more variable within species than other compartments and might be influenced by other non-measured predictors. Furthermore, tree height, crown length and WSG only marginally improved mixed-species model ADs, hence underlining the poor capacity of those predictors in describing differences in root biomass among species.

Finally, models predicting TAB and TB reported moderate AD reductions by fitting species-specific compared with mixed-species models, but this might be due to the good performance of the mixed-species models which accounted for 97 to 99 percent of data variability and reported ADs of 15 to 25 percent. In comparison, species-specific models explained 95 to almost 100 percent of data variability and reported ADs of 8 to 21 percent. These models can still be valuable for studies at species level requiring the most precise predictions possible. Model performance and AD reductions by fitting species-specific models were consistent and similar to values reported in Nelson et al. (1999), Wang (2006) and Basuki et al. (2009).

It is worth noting that LME final models were characterised by slightly lower ADs if they included exactly the same predictors as the LM models (Table 3–9). This statistical advantage is probably due to the lower sensibility of LME to extreme values. On the other hand, most of the LM final models (containing generally more predictors than the LME models) reported

lower ADs than the corresponding minimal LME models. Therefore, the necessity of using sophisticated LME models may be questionable. However, LM models are fitted in order to mathematically minimize the errors, while LME model additionally fit the random term on a normal distribution, thus pulling the estimations toward the grand mean (Gelman & Hill 2007). Consequently, LM models fit more precisely the data they were fit on while LME models are likely to make better predictions for other species. Because the eight tree species used in the present study represent the three most common functional groups of trees in these forests, the mixed-species LME models are likely to produce estimations capable of evaluating other species.

In summary, we suggest to use species-specific models when the predictions have to be done for the same species and to use LME mixed-species models when the predictions have to be done for different (or groups containing different) species. We do not recommend using the functional group species models, as these did not markedly improve model fit.

*Scaling-up predictions to forest plots*

Individual predicted biomass ADs compensate for each other when the model is applied to plots containing several trees, so that the plot AD is smaller than individual ADs (see equation 7). Plot AD is also sensitive to tree size: biomass estimates are squared resulting in a disproportional contribution of the large values. In other words, the larger the trees, the larger the total biomass uncertainty of the plot (Chave et al. 2014). Such a system is relevant because large trees contribute the most to plot biomass, so the contribution to plot error is related to the contribution to plot biomass.

The mixed-species LME model used to calculate plot TB was characterized by an AD of 23.7%. Plot ADs ranged from 3.2% to 9.4%. As seen above, plot AD is sensitive to the number of trees. In this study, the plots with greater AD contained only 20 trees whereas the average number of trees in the plots was 61.

The other error type is the bias: a systematic error depending mainly on data quality used to estimate the model parameters. Because the bias can vary with tree size, its action also depends on the target tree size. Therefore, plot prediction accuracy depends in part on the range and evenness of DBH of the trees used to calculate the model parameters and on the other side the DBH distribution of the trees in the plots. In the example provided in this study, the mixed-species LME model contained a significant average bias of 6.2% ($p=0.020$, Fig 2), also significantly ($p=0.013$) influenced by tree DBH. For instance, the trees used to fit the model were on average overestimated by 6.2%. The small trees tended to be overestimated while the big trees tended to be underestimated. The bias is estimated to be null for trees of 19 cm of DBH, implying that if each tree in the plots had a DBH of 19 cm, their predicted biomass would have no bias. As seen in Figure 4, the size distribution of the trees used to fit the model was similar to the size distribution of the estimated trees. Consequently, the predicted values should be characterized by similar bias and ADs as the original values. Biases must also be considered as warnings: if a model is used outside the original data range or on single-sized trees, biases could lead to sever under or overestimation of biomass.

**Conclusion**

Biomass prediction quality was variable but TB and TAB were predicted accurately. Different factors differentially affected the various biomass compartments, hence justifying the use of separate equations depending on the scope, the tree species, and the data availability of the study. Leaf biomass was variable within and among species, resulting in poor prediction accuracy.

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**Tables**

Table 1. The eight tree species investigated in this study

| Species | species abbreviation | Family | Functional group | n | DBH range (cm) |
|---|---|---|---|---|---|
| *Alniphyllum fortunei* (Hemsley, 1906) | Alf | Styracaceae | d | 21 | 3.4-18.7 |
| *Castanopsis fargesii* (Morot, 1899) | Caf | Fagaceae | e | 25 | 2.5-27.3 |
| *Castanopsis sclerophylla* (Lindley & Paxton, 1912) | Cas | Fagaceae | e | 16 | 2.7-16.1 |
| *Cunninghamia lanceolata* (Lambert, 1827) | Cul | Taxodiaceae | c | 17 | 1-17.7 |
| *Liquidambar formosana* (Hance, 1886) | Lif | Hamamelidaceae | d | 15 | 2.6-37.5 |
| *Pinus massoniana* (Lambert, 1803) | Pim | Pinaceae | c | 19 | 2.9-23.2 |
| *Sassafras tzumu* (Hemsley, 1907) | Sat | Lauraceae | d | 20 | 5.1-27.7 |
| *Schima superba* (Gardner & Champion, 1849) | Scs | Theaceae | e | 21 | 1.2-23.1 |

Note: deciduous broadleaf: d, evergreen broadleaf: e, evergreen coniferous: c

Table 2. Initial models

| Pred | Initial model | Rational |
|---|---|---|
| 4 | $log(biomass) = \beta_0 + \beta_1 lnDBH + \beta_2 lnH + \beta_3 lnC + \beta_4 WSG$ | All predictors are known |
| 3 | $log(biomass) = \beta_0 + \beta_1 lnDBH + \beta_2 lnH + \beta_3 WSG$ | Often the crown length is not measured in surveys |
| 2 | $log(biomass) = \beta_0 + \beta_1 lnDBH + \beta_2 lnH$ | The species identity is unknown |
| 2’ | $log(biomass) = \beta_0 + \beta_1 lnDBH + \beta_2 WSG$ | Tree height is often not measured but species identity is known |
| 1 | $log(biomass) = \beta_0 + \beta_1 lnDBH$ | Only DBH is measured |

Pred: number of predictors in the initial model, lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

Table 3. Best models (see methods for details) for the estimation of leaf biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4, 3, 2, 2', 1 | *lnlf ~ lnDBH* | 154 | 0.75 | 0.478 | 92.5 |
| LM | All species | 4 | *lnlf ~ lnDBH + lnH + lnC + WSG* | 154 | 0.82 | 0.685 | 85.2 |
| | | 3 | *lnlf ~ lnDBH + lnH + WSG* | 154 | 0.79 | 0.737 | 103.9 |
| | | 2 | *lnlf ~ lnDBH + lnH* | 154 | 0.75 | 0.790 | 116.9 |
| | | 2' | *lnlf ~ lnDBH + WSG* | 154 | 0.78 | 0.754 | 107.3 |
| | | 1 | *lnlf ~ lnDBH* | 154 | 0.75 | 0.800 | 119.4 |
| LME | Deciduous | 4, 3, 2 | *lnlf ~ lnDBH + lnH* | 56 | 0.89 | 0.463 | 56.2 |
| | | 2', 1 | *lnlf ~ lnDBH* | 56 | 0.88 | 0.481 | 60.8 |
| LM | Deciduous | 4 | *lnlf ~ lnDBH + lnC* | 56 | 0.90 | 0.507 | 50.9 |
| | | 3, 2, 2', 1 | *lnlf ~ lnDBH* | 56 | 0.88 | 0.547 | 61.3 |
| LME | Evergreen | 4, 3, 2, 2', 1 | *lnlf ~ lnDBH* | 62 | 0.92 | 0.379 | 36.0 |
| LM | Evergreen | 4, 3, 2' | *lnlf ~ lnDBH + WSG* | 62 | 0.93 | 0.408 | 35.6 |
| | | 2, 1 | *lnlf ~ lnDBH* | 62 | 0.92 | 0.420 | 37.5 |
| LME | Coniferous | 4, 3, 2 | *lnlf ~ lnDBH + lnH* | 36 | 0.84 | 0.522 | 54.9 |
| | | 2' | *lnlf ~ lnDBH + WSG* | 36 | NA | 0.531 | 50.6 |
| | | 1 | *lnlf ~ lnDBH* | 36 | 0.79 | 0.524 | 64.0 |
| LM | Coniferous | 4, 3 | *lnlf ~ lnDBH + lnH + WSG* | 36 | 0.85 | 0.530 | 49.7 |
| | | 2 | *lnlf ~ lnDBH + lnH* | 36 | 0.84 | 0.559 | 56.6 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 2’ | *lnlf ~ lnDBH + WSG* | 36 | 0.85 | 0.531 | 50.6 |
| | | 1 | *lnlf ~ lnDBH* | 36 | 0.79 | 0.633 | 69.5 |
| LM | Alf | 3, 2, 1 | *lnlf ~ lnDBH* | 21 | 0.92 | 0.409 | 38.6 |
| LM | Lif | 3, 2, 1 | *lnlf ~ lnDBH* | 15 | 0.96 | 0.370 | 28.6 |
| LM | Sat | 3, 2 | *lnlf ~ lnDBH + lnH* | 20 | 0.84 | 0.500 | 43.9 |
| | | 1 | *lnlf ~ lnDBH* | 20 | 0.74 | 0.630 | 74.5 |
| LM | Caf | 3, 2 | *lnlf ~ lnDBH + lnH* | 25 | 0.96 | 0.295 | 21.4 |
| | | 1 | *lnlf ~ lnDBH* | 25 | 0.94 | 0.339 | 27.2 |
| LM | Cas | 3, 2, 1 | *lnlf ~ lnDBH* | 16 | 0.87 | 0.492 | 45.8 |
| LM | Scs | 3 | *lnlf ~ lnDBH + lnH + lnC* | 21 | 0.97 | 0.251 | 20.9 |
| | | 2, 1 | *lnlf ~ lnDBH* | 21 | 0.96 | 0.319 | 26.5 |
| LM | Cul | 3, 2, 1 | *lnlf ~ lnDBH* | 17 | 0.85 | 0.553 | 53.1 |
| LM | Pim | 3, 2, 1 | *lnlf ~ lnDBH* | 19 | 0.90 | 0.444 | 39.5 |

Note: Model type is either a linear model (LM) or a mixed linear model (LME); for the species names see Table 1, Pred: number of predictors in the initial model. lnlf: log of leaf biomass (kg), lnDBH: log of diameter at breast height (cm). lnH: log of tree height (m). lnC: log of crown length (m). WSG: wood specific gravity (g $cm^{-3}$). N: number of tree. $R^2$: adjusted $r^2$. One $R^2$=NA because the lmmfit function does not work with ASReml.

Table 4. Best models (see methods for details) for the estimation branch wood biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4 | *lnbr ~ lnDBH + lnC + WSG* | 147 | 0.94 | 0.404 | 44.8 |
| | | 3, 2’ | *lnbr ~ lnDBH + WSG* | 147 | 0.93 | 0.411 | 47.4 |
| | | 2, 1 | *lnbr ~ lnDBH* | 147 | 0.89 | 0.411 | 61.8 |
| LM | All species | 4 | *lnbr ~ lnDBH + lnC + WSG* | 147 | 0.94 | 0.451 | 44.9 |
| | | 3, 2’ | *lnbr ~ lnDBH + WSG* | 147 | 0.93 | 0.465 | 47.9 |
| | | 2, 1 | *lnbr ~ lnDBH* | 147 | 0.89 | 0.595 | 69.0 |
| LME | Deciduous | 4, 3, 2’, 2, 1 | *lnbr ~ lnDBH* | 56 | 0.91 | 0.462 | 66.4 |
| LM | Deciduous | 4 | *lnbr ~ lnDBH + lnC + WSG* | 56 | 0.93 | 0.501 | 54.5 |
| | | 3, 2’ | *lnbr ~ lnDBH + WSG* | 56 | 0.92 | 0.534 | 60.1 |
| | | 2, 1 | *lnbr ~ lnDBH* | 56 | 0.91 | 0.588 | 68.0 |
| LME | Evergreen | 4 | *lnbr ~ lnDBH + lnH +lnC* | 57 | 0.96 | 0.357 | 32.5 |
| | | 3, 2, 2’, 1 | *lnbr ~ lnDBH* | 57 | 0.95 | 0.380 | 36.3 |
| LM | Evergreen | 4 | *lnbr ~ lnDBH + lnH + lnC* | 57 | 0.95 | 0.372 | 32.8 |
| | | 3, 2’ | *lnbr ~ lnDBH + WSG* | 57 | 0.95 | 0.380 | 33.2 |
| | | 2, 1 | *lnbr ~ lnDBH* | 57 | 0.95 | 0.399 | 36.8 |
| LME | Coniferous | 4 | *lnbr ~ lnDBH + lnC + WSG* | 34 | NA | 0.351 | 30.3 |
| | | 3, 2’ | *lnbr ~ lnDBH + WSG* | 34 | NA | 0.364 | 32.2 |
| | | 2, 1 | *lnbr ~ lnDBH* | 34 | 0.92 | 0.358 | 44.7 |
| LM | Coniferous | 4 | *lnbr ~ lnDBH + lnH + lnC + WSG* | 34 | 0.96 | 0.331 | 27.1 |
| | | 3 | *lnbr ~ lnDBH + lnH + WSG* | 34 | 0.95 | 0.370 | 32.2 |
| | | 2 | *lnbr ~ lnDBH + lnH* | 34 | 0.93 | 0.427 | 39.9 |
| | | 2’ | *lnbr ~ lnDBH + WSG* | 34 | 0.95 | 0.364 | 32.2 |
| | | 1 | *lnbr ~ lnDBH* | 34 | 0.92 | 0.474 | 46.4 |
| LM | Alf | 3, 2, 1 | *lnbr ~ lnDBH* | 21 | 0.94 | 0.416 | 38.0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| LM | Lif | 3, 2, 1 | *lnbr ~ lnDBH* | 15 | 0.98 | 0.299 | 25.8 |
| LM | Sat | 3, 2 | *lnbr ~ lnDBH + lnH* | 20 | 0.84 | 0.553 | 56.7 |
| | | 1 | *lnbr ~ lnDBH* | 20 | 0.81 | 0.614 | 72.3 |
| LM | Caf | 3 | *lnbr ~ lnDBH + lnH + lnC* | 21 | 0.98 | 0.188 | 13.3 |
| | | 2 | *lnbr ~ lnDBH + lnH* | 21 | 0.97 | 0.231 | 17.8 |
| | | 1 | *lnbr ~ lnDBH* | 21 | 0.96 | 0.265 | 21.7 |
| LM | Cas | 3, 2, 1 | *lnbr ~ lnDBH* | 16 | 0.91 | 0.460 | 41.9 |
| LM | Scs | 3 | *lnbr ~ lnDBH + lnH + lnC* | 20 | 0.96 | 0.353 | 26.7 |
| | | 2, 1 | *lnbr ~ lnDBH* | 20 | 0.95 | 0.432 | 39.0 |
| LM | Cul | 3 | *lnbr ~ lnDBH + lnH + lnC* | 15 | 0.94 | 0.353 | 27.0 |
| | | 2, 1 | *lnbr ~ lnDBH* | 15 | 0.91 | 0.442 | 43.4 |
| LM | Pim | 3 | *lnbr ~ lnDBH + lnH + lnC* | 19 | 0.98 | 0.238 | 17.3 |
| | | 2 | *lnbr ~ lnDBH + lnH* | 19 | 0.97 | 0.268 | 19.8 |
| | | 1 | *lnbr ~ lnDBH* | 19 | 0.96 | 0.301 | 23.8 |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lnbr: log of branch wood biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$. Two $R^2$=NA because the lmmfit function does not work with ASReml.

Table 5. Best models (see methods for details) for the estimation stem wood biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4 | *lnstem ~ lnDBH + lnH + lnC + WSG* | 147 | 0.99 | 0.137 | 12.9 |
| | | 3 | *lnstem ~ lnDBH + lnH + WSG* | 147 | 0.99 | 0.143 | 12.6 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 147 | 0.98 | 0.143 | 15.4 |
| | | 2’ | *lnstem ~ lnDBH + WSG* | 147 | 0.97 | 0.196 | 18.8 |
| | | 1 | *lnstem ~ lnDBH* | 147 | 0.97 | 0.196 | 21.8 |
| LM | All species | 4, 3 | *lnstem ~ lnDBH + lnH + WSG* | 147 | 0.99 | 0.157 | 12.6 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 147 | 0.98 | 0.192 | 15.8 |
| | | 2’ | *lnstem ~ lnDBH + WSG* | 147 | 0.97 | 0.235 | 19.0 |
| | | 1 | *lnstem ~ lnDBH* | 147 | 0.97 | 0.270 | 22.2 |
| LME | Deciduous | 4, 3, 2 | *lnstem ~ lnDBH + lnH* | 56 | 0.99 | 0.141 | 13.0 |
| | | 2’, 1 | *lnstem ~ lnDBH* | 56 | 0.98 | 0.192 | 17.4 |
| LM | Deciduous | 4, 3 | *lnstem ~ lnDBH + lnH + WSG* | 56 | 0.99 | 0.143 | 11.4 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 56 | 0.99 | 0.164 | 13.0 |
| | | 2’ | *lnstem ~ lnDBH + WSG* | 56 | 0.98 | 0.193 | 15.8 |
| | | 1 | *lnstem ~ lnDBH* | 56 | 0.98 | 0.206 | 17.3 |
| LME | Evergreen | 4 | *lnstem ~ lnDBH + lnH + lnC* | 57 | 0.99 | 0.127 | 9.8 |
| | | 3, 2 | *lnstem ~ lnDBH + lnH* | 57 | 0.99 | 0.141 | 10.7 |
| | | 2’, 1 | *lnstem ~ lnDBH* | 57 | 0.98 | 0.193 | 15.1 |
| LM | Evergreen | 4 | *lnstem ~ lnDBH + lnH + lnC* | 57 | 0.99 | 0.132 | 9.8 |
| | | 3, 2 | *lnstem ~ lnDBH + lnH* | 57 | 0.99 | 0.145 | 10.8 |
| | | 2’, 1 | *lnstem ~ lnDBH* | 57 | 0.98 | 0.198 | 15.1 |
| LME | Coniferous | 4 | *lnstem ~ lnDBH + lnH + lnC + WSG* | 34 | NA | 0.142 | 11.1 |
| | | 3 | *lnstem ~ lnDBH + lnH + WSG* | 34 | NA | 0.145 | 11.3 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 34 | 0.98 | 0.141 | 14.4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 2’ | *lnstem ~ lnDBH + WSG* | 34 | NA | 0.195 | 15.7 |
| | | 1 | *lnstem ~ lnDBH* | 34 | 0.94 | 0.192 | 26.9 |
| LM | Coniferous | 4 | *lnstem ~ lnDBH + lnH + lnC + WSG* | 34 | 0.99 | 0.142 | 11.1 |
| | | 3 | *lnstem ~ lnDBH + lnH + WSG* | 34 | 0.99 | 0.145 | 11.3 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 34 | 0.98 | 0.169 | 12.8 |
| | | 2’ | *lnstem ~ lnDBH + WSG* | 34 | 0.98 | 0.195 | 15.7 |
| | | 1 | *lnstem ~ lnDBH* | 34 | 0.94 | 0.317 | 27.9 |
| LM | Alf | 3, 2 | *lnstem ~ lnDBH + lnH* | 21 | 0.99 | 0.114 | 8.3 |
| | | 1 | *lnstem ~ lnDBH* | 21 | 0.99 | 0.151 | 12.8 |
| LM | Lif | 3, 2 | *lnstem ~ lnDBH + lnH* | 15 | 0.99 | 0.142 | 10.5 |
| | | 1 | *lnstem ~ lnDBH* | 15 | 0.99 | 0.195 | 15.6 |
| LM | Sat | 3, 2 | *lnstem ~ lnDBH + lnH* | 20 | 0.98 | 0.130 | 9.8 |
| | | 1 | *lnstem ~ lnDBH* | 20 | 0.96 | 0.186 | 14.4 |
| LM | Caf | 3 | *lnstem ~ lnDBH + lnH + lnC* | 21 | 0.99 | 0.084 | 6.4 |
| | | 2 | *lnstem ~ lnDBH + lnH* | 21 | 0.99 | 0.111 | 8.7 |
| | | 1 | *lnstem ~ lnDBH* | 21 | 0.99 | 0.126 | 9.4 |
| LM | Cas | 3, 2 | *lnstem ~ lnDBH + lnH* | 16 | 0.99 | 0.150 | 9.7 |
| | | 1 | *lnstem ~ lnDBH* | 16 | 0.98 | 0.203 | 12.9 |
| LM | Scs | 3, 2 | *lnstem ~ lnDBH + lnH* | 20 | 0.99 | 0.175 | 13.2 |
| | | 1 | *lnstem ~ lnDBH* | 20 | 0.98 | 0.221 | 17.4 |
| LM | Cul | 3, 2 | *lnstem ~ lnDBH + lnH* | 15 | 0.98 | 0.156 | 11.1 |
| | | 1 | *lnstem ~ lnDBH* | 15 | 0.98 | 0.191 | 16.1 |
| LM | Pim | 3, 2 | *lnstem ~ lnDBH + lnH* | 19 | 0.99 | 0.126 | 9.8 |
| | | 1 | *lnstem ~ lnDBH* | 19 | 0.98 | 0.191 | 15.0 |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lnstem: log of stem wood biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$. Three $R^2$=NA because the lmmfit function does not work with ASReml.

Table 6. Best models (see methods for details) for the estimation dead attached material biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4, 3, 2, 2', 1 | *lndam ~ lnDBH* | 154 | 0.41 | 1.720 | 7960 |
| LM | All species | 4, 3, 2' | *lndam ~ lnDBH + WSG* | 154 | 0.42 | 2.030 | 12107 |
| | | 2, 1 | *lndam ~ lnDBH* | 154 | 0.40 | 2.061 | 14975 |
| LME | Deciduous | 4, 3, 2, 2', 1 | *lndam ~ lnDBH* | 56 | 0.36 | 2.016 | 12553 |
| LM | Deciduous | 4, 3, 2' | *lndam ~ lnDBH + WSG* | 56 | 0.45 | 2.210 | 14091 |
| | | 2, 1 | *lndam ~ lnDBH* | 56 | 0.37 | 2.356 | 31635 |
| LME | Evergreen | 4, 3, 2, 2', 1 | *lndam ~ lnDBH* | 62 | 0.38 | 1.589 | 6189 |
| LM | Evergreen | 4, 3, 2, 2', 1 | *lndam ~ lnDBH* | 62 | 0.38 | 1.914 | 8229 |
| LME | Coniferous | 4, 3, 2 | *lndam ~ lnDBH + lnH* | 36 | 0.72 | 1.340 | 933.2 |
| | | 2', 1 | *lndam ~ lnDBH* | 36 | 0.66 | 1.381 | 1664 |
| LM | Coniferous | 4, 3, 2 | *lndam ~ lnDBH + lnH* | 36 | 0.70 | 1.400 | 1017 |
| | | 2' | *lndam ~ lnDBH + WSG* | 36 | 0.70 | 1.400 | 1040 |
| | | 1 | *lndam ~ lnDBH* | 36 | 0.66 | 1.493 | 1949 |
| LM | Alf | 3, 2, 1 | *lndam ~ 1* | 21 | NA | 2.459 | 9124 |
| LM | Lif | 3, 2, 1 | *lndam ~ lnDBH* | 15 | 0.51 | 2.035 | 6307 |
| LM | Sat | 3, 2, 1 | *lndam ~ lnDBH* | 20 | 0.28 | 1.390 | 2298 |
| LM | Caf | 3, 2, 1 | *lndam ~ lnDBH* | 25 | 0.42 | 2.021 | 7936 |
| LM | Cas | 3, 2, 1 | *lndam ~ lnDBH* | 16 | 0.35 | 1.134 | 255.9 |
| LM | Scs | 3, 2, 1 | *lndam ~ lnDBH* | 21 | 0.72 | 1.306 | 700.0 |
| LM | Cul | 3, 2, 1 | *lndam ~ lnDBH* | 17 | 0.57 | 1.913 | 4641 |
| LM | Pim | 3 | *lndam ~ lnDBH + lnC* | 19 | 0.82 | 0.620 | 62.2 |
| | | 2, 1 | *lndam ~ lnDBH* | 19 | 0.77 | 0.707 | 85.1 |

Note: Model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lndam: log of dead attached material biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$. One $R^2$=NA because no variables were significant.

Table 7. Best models (see methods for details) for the estimation root biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4, 3, 2 | *lnroot ~ lnDBH + lnH* | 154 | 0.91 | 0.409 | 44.3 |
| | | 2', 1 | *lnroot ~ lnDBH* | 154 | 0.91 | 0.424 | 46.3 |
| LM | All species | 4 | *lnroot ~ lnDBH + lnH + lnC + WSG* | 154 | 0.92 | 0.475 | 43.0 |
| | | 3 | *lnroot ~ lnDBH + lnH + WSG* | 154 | 0.92 | 0.476 | 43.1 |
| | | 2 | *lnroot ~ lnDBH + lnH* | 154 | 0.91 | 0.496 | 46.0 |
| | | 2' | *lnroot ~ lnDBH + WSG* | 154 | 0.91 | 0.484 | 44.7 |
| | | 1 | *lnroot ~ lnDBH* | 154 | 0.91 | 0.502 | 47.9 |
| LME | Deciduous | 4, 3, 2, 2', 1 | *lnroot ~ lnDBH* | 56 | 0.93 | 0.326 | 37.2 |
| LM | Deciduous | 4 | *lnroot ~ lnDBH + lnH + lnC + WSG* | 56 | 0.95 | 0.363 | 29.6 |
| | | 3, 2' | *lnroot ~ lnDBH + WSG* | 56 | 0.95 | 0.384 | 32.8 |
| | | 2, 1 | *lnroot ~ lnDBH* | 56 | 0.93 | 0.438 | 37.1 |
| LME | Evergreen | 4, 3, 2 | *lnroot ~ lnDBH + lnH* | 62 | 0.93 | 0.430 | 39.3 |
| | | 2', 1 | *lnroot ~ lnDBH* | 62 | 0.92 | 0.455 | 44.6 |
| LM | Evergreen | 4, 3, 2 | *lnroot ~ lnDBH + lnH* | 62 | 0.93 | 0.447 | 39.7 |
| | | 2', 1 | *lnroot ~ lnDBH* | 62 | 0.92 | 0.473 | 44.9 |
| LME | Coniferous | 4, 3, 2, 2', 1 | *lnroot ~ lnDBH* | 36 | 0.91 | 0.430 | 36.6 |
| LM | Coniferous | 4, 3, 2, 2', 1 | *lnroot ~ lnDBH* | 36 | 0.91 | 0.443 | 36.8 |
| LM | Alf | 3, 2, 1 | *lnroot ~ lnDBH* | 21 | 0.96 | 0.289 | 23.3 |
| LM | Lif | 3, 2, 1 | *lnroot ~ lnDBH* | 15 | 0.94 | 0.435 | 37.0 |
| LM | Sat | 3, 2, 1 | *lnroot ~ lnDBH* | 20 | 0.97 | 0.204 | 16.5 |
| LM | Caf | 3, 2 | *lnroot ~ lnDBH + lnH* | 25 | 0.92 | 0.480 | 40.5 |
| | | 1 | *lnroot ~ lnDBH* | 25 | 0.89 | 0.566 | 56.7 |
| LM | Cas | 3, 2, 1 | *lnroot ~ lnDBH* | 16 | 0.95 | 0.259 | 21.4 |
| LM | Scs | 3, 2, 1 | *lnroot ~ lnDBH* | 21 | 0.95 | 0.433 | 36.5 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| LM | Cul | 3, 2, 1 | *lnroot ~ lnDBH* | 17 | 0.90 | 0.432 | 41.3 |
| LM | Pim | 3, 2 | *lnroot ~ lnDBH + lnH* | 19 | 0.98 | 0.224 | 18.9 |
| | | 1 | *lnroot ~ lnDBH* | 19 | 0.97 | 0.252 | 20.6 |

Note: Model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lnroot: log of root biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$.

Table 8. Best models (see methods for details) for the estimation total above-ground biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4 | *lnTAB ~ lnDBH + lnH + lnC + WSG* | 154 | 0.99 | 0.179 | 14.8 |
| | | 3 | *lnTAB ~ lnDBH + lnH + WSG* | 154 | 0.99 | 0.179 | 15.1 |
| | | 2 | *lnTAB ~ lnDBH + lnH* | 154 | 0.98 | 0.179 | 22.4 |
| | | 2’ | *lnTAB ~ lnDBH + WSG* | 154 | 0.98 | 0.190 | 16.6 |
| | | 1 | *lnTAB ~ lnDBH* | 154 | 0.97 | 0.190 | 24.0 |
| LM | All species | 4 | *lnTAB ~ lnDBH + lnH + lnC + WSG* | 154 | 0.99 | 0.197 | 15.2 |
| | | 3 | *lnTAB ~ lnDBH + lnH + WSG* | 154 | 0.99 | 0.201 | 15.2 |
| | | 2 | *lnTAB ~ lnDBH + lnH* | 154 | 0.97 | 0.276 | 23.0 |
| | | 2’ | *lnTAB ~ lnDBH + WSG* | 154 | 0.98 | 0.214 | 16.7 |
| | | 1 | *lnTAB ~ lnDBH* | 154 | 0.97 | 0.291 | 24.6 |
| LME | Deciduous | 4, 3, 2 | *lnTAB ~ lnDBH + lnH* | 56 | 0.98 | 0.145 | 16.5 |
| | | 2’, 1 | *lnTAB ~ lnDBH* | 56 | 0.98 | 0.187 | 18.8 |
| LM | Deciduous | 4 | *lnTAB ~ lnDBH + lnH + lnC + WSG* | 56 | 0.99 | 0.160 | 12.7 |
| | | 3 | *lnTAB ~ lnDBH + lnH + WSG* | 56 | 0.99 | 0.162 | 12.9 |
| | | 2 | *lnTAB ~ lnDBH + lnH* | 56 | 0.98 | 0.195 | 16.5 |
| | | 2’ | *lnTAB ~ lnDBH + WSG* | 56 | 0.98 | 0.199 | 15.9 |
| | | 1 | *lnTAB ~ lnDBH* | 56 | 0.98 | 0.224 | 18.6 |
| LME | Evergreen | 4, 3, 2, 2’, 1 | *lnTAB ~ lnDBH* | 62 | 0.99 | 0.170 | 13.1 |
| LM | Evergreen | 4, 3, 2, 2’, 1 | *lnTAB ~ lnDBH* | 62 | 0.99 | 0.177 | 13.3 |
| LME | Coniferous | 4, 3 | *lnTAB ~ lnDBH + lnH + WSG* | 36 | NA | 0.200 | 13.3 |
| | | 2, 1 | *lnTAB ~ lnDBH* | 36 | 0.96 | 0.202 | 28.9 |
| | | 2’ | *lnTAB ~ lnDBH + WSG* | 36 | NA | 0.205 | 14.5 |
| LM | Coniferous | 4, 3 | *lnTAB ~ lnDBH + lnH + WSG* | 36 | 0.99 | 0.201 | 13.3 |
| | | 2 | *lnTAB ~ lnDBH + lnH* | 36 | 0.98 | 0.240 | 19.1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 2’ | *lnTAB ~ lnDBH + WSG* | 36 | 0.98 | 0.205 | 14.5 |
| | | 1 | *lnTAB ~ lnDBH* | 36 | 0.97 | 0.309 | 27.6 |
| LM | Alf | 3, 2 | *lnTAB ~ lnDBH + lnH* | 21 | 0.99 | 0.110 | 8.2 |
| | | 1 | *lnTAB ~ lnDBH* | 21 | 0.99 | 0.130 | 10.6 |
| LM | Lif | 3, 2 | *lnTAB ~ lnDBH + lnH* | 15 | 1.00 | 0.115 | 8.5 |
| | | 1 | *lnTAB ~ lnDBH* | 15 | 0.99 | 0.140 | 10.1 |
| LM | Sat | 3, 2 | *lnTAB ~ lnDBH + lnH* | 20 | 0.98 | 0.148 | 11.4 |
| | | 1 | *lnTAB ~ lnDBH* | 20 | 0.95 | 0.217 | 17.3 |
| LM | Caf | 3, 2, 1 | *lnTAB ~ lnDBH* | 25 | 1.00 | 0.108 | 8.6 |
| LM | Cas | 3, 2, 1 | *lnTAB ~ lnDBH* | 16 | 0.98 | 0.194 | 12.6 |
| LM | Scs | 3 | *lnTAB ~ lnDBH + lnC* | 21 | 0.99 | 0.196 | 14.5 |
| | | 2, 1 | *lnTAB ~ lnDBH* | 21 | 0.99 | 0.214 | 15.8 |
| LM | Cul | 3, 2, 1 | *lnTAB ~ lnDBH* | 17 | 0.98 | 0.238 | 17.1 |
| LM | Pim | 3, 2 | *lnTAB ~ lnDBH + lnH* | 19 | 0.99 | 0.110 | 7.7 |
| | | 1 | *lnTAB ~ lnDBH* | 19 | 0.98 | 0.172 | 13.1 |

Note: Model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lnTAB: log of total above-ground biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$. Two $R^2$=NA because the lmmfit function does not work with ASReml.

Table 9. biomass best models (see methods for details) for the estimation total biomass according to the number of predictors

| Type | Species/group of species | Pred. | Allometric equation | N | $R^2$ | Residual standard error | Average deviation |
|---|---|---|---|---|---|---|---|
| LME | All species | 4, 3 | *lnTB ~ lnDBH + lnH + WSG* | 154 | 0.98 | 0.200 | 17.2 |
| | | 2 | *lnTB ~ lnDBH + lnH* | 154 | 0.97 | 0.200 | 23.3 |
| | | 2’ | *lnTB ~ lnDBH + WSG* | 154 | 0.98 | 0.204 | 17.4 |
| | | 1 | *lnTB ~ lnDBH* | 154 | 0.97 | 0.204 | 23.7 |
| LM | All species | 4 | *lnTB ~ lnDBH + lnH + lnC + WSG* | 154 | 0.98 | 0.224 | 17.1 |
| | | 3 | *lnTB ~ lnDBH + lnH + WSG* | 154 | 0.98 | 0.228 | 17.4 |
| | | 2 | *lnTB ~ lnDBH + lnH* | 154 | 0.97 | 0.290 | 24.0 |
| | | 2’ | *lnTB ~ lnDBH + WSG* | 154 | 0.98 | 0.232 | 17.6 |
| | | 1 | *lnTB ~ lnDBH* | 154 | 0.97 | 0.296 | 24.2 |
| LME | Deciduous | 4, 3, 2 | *lnTB ~ lnDBH + lnH* | 56 | 0.98 | 0.150 | 19.3 |
| | | 2’, 1 | *lnTB ~ lnDBH* | 56 | 0.98 | 0.177 | 20.4 |
| LM | Deciduous | 4 | *lnTB ~ lnDBH + lnH + lnC + WSG* | 56 | 0.99 | 0.173 | 14.5 |
| | | 3 | *lnTB ~ lnDBH + lnH + WSG* | 56 | 0.99 | 0.180 | 15.0 |
| | | 2 | *lnTB ~ lnDBH + lnH* | 56 | 0.98 | 0.225 | 19.1 |
| | | 2’ | *lnTB ~ lnDBH + WSG* | 56 | 0.98 | 0.203 | 16.1 |
| | | 1 | *lnTB ~ lnDBH* | 56 | 0.98 | 0.241 | 20.0 |
| LME | Evergreen | 4, 3, 2, 2’, 1 | *lnTB ~ lnDBH* | 62 | 0.99 | 0.181 | 14.7 |
| LM | Evergreen | 4, 3, 2’ | *lnTB ~ lnDBH + WSG* | 62 | 0.99 | 0.182 | 13.9 |
| | | 2, 1 | *lnTB ~ lnDBH* | 62 | 0.99 | 0.189 | 14.9 |
| LME | Coniferous | 4, 3, 2’ | *lnTB ~ lnDBH + WSG* | 36 | NA | 0.232 | 16.6 |
| | | 2, 1 | *lnTB ~ lnDBH* | 36 | 0.97 | 0.229 | 26.3 |
| LM | Coniferous | 4, 3 | *lnTB ~ lnDBH + lnH + WSG* | 36 | 0.98 | 0.235 | 16.4 |
| | | 2 | *lnTB ~ lnDBH + lnH* | 36 | 0.97 | 0.263 | 20.7 |
| | | 2’ | *lnTB ~ lnDBH + WSG* | 36 | 0.98 | 0.232 | 16.6 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | *lnTB ~ lnDBH* | 36 | 0.97 | 0.290 | 24.4 |
| LM | Alf | 3, 2, 1 | *lnTB ~ lnDBH* | 21 | 0.99 | 0.127 | 10.6 |
| LM | Lif | 3, 2 | *lnTB ~ lnDBH + lnH* | 15 | 0.99 | 0.147 | 12.1 |
| | | 1 | *lnTB ~ lnDBH* | 15 | 0.99 | 0.186 | 14.9 |
| LM | Sat | 3, 2 | *lnTB ~ lnDBH + lnH* | 20 | 0.98 | 0.150 | 11.6 |
| | | 1 | *lnTB ~ lnDBH* | 20 | 0.96 | 0.199 | 15.9 |
| LM | Caf | 3, 2, 1 | *lnTB ~ lnDBH* | 25 | 0.99 | 0.155 | 11.6 |
| LM | Cas | 3, 2, 1 | *lnTB ~ lnDBH* | 16 | 0.98 | 0.181 | 11.7 |
| LM | Scs | 3, 2, 1 | *lnTB ~ lnDBH* | 21 | 0.99 | 0.214 | 17.2 |
| LM | Cul | 3, 2, 1 | *lnTB ~ lnDBH* | 17 | 0.97 | 0.264 | 20.5 |
| LM | Pim | 3, 2 | *lnTB ~ lnDBH + lnH* | 19 | 0.99 | 0.104 | 7.1 |
| | | 1 | *lnTB ~ lnDBH* | 19 | 0.98 | 0.166 | 13.4 |

Note: Model type is either a linear model (LM) or a mixed linear model (LME), for the species names see Table 1, Pred: number of predictors in the initial model. lnTB: log of total biomass (kg), lnDBH: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$), N: number of tree, $R^2$: adjusted $r^2$. One $R^2$=NA because the lmmfit function does not work with ASReml.

Table 10. Total biomasses of the comparative study plots estimated with LME model

| CSP | Biomass (kg) | AD (%) |
|---|---|---|
| 1 | 10773 | 4.5 |
| 2 | 10868 | 5.2 |
| 3 | 8514 | 3.6 |
| 4 | 20514 | 4.6 |
| 5 | 17582 | 3.8 |
| 6 | 7154 | 5.1 |
| 7 | 13959 | 4.1 |
| 8 | 15527 | 3.3 |
| 9 | 15616 | 4.6 |
| 10 | 17232 | 4.1 |
| 11 | 13228 | 3.2 |
| 12 | 26372 | 3.8 |
| 13 | 15513 | 5.1 |
| 14 | 28805 | 4.7 |
| 15 | 21451 | 3.6 |
| 16 | 5186 | 4.8 |
| 17 | 4673 | 4.6 |
| 18 | 21563 | 4.4 |
| 21 | 12724 | 9.3 |
| 22 | 1018 | 7.5 |
| 23 | 7661 | 8.3 |
| 24 | 6202 | 9.4 |
| 25 | 5801 | 3.8 |
| 26 | 4486 | 4.2 |
| 27 | 29240 | 3.4 |

Note: AD is the estimated plot average deviation

**Figures**

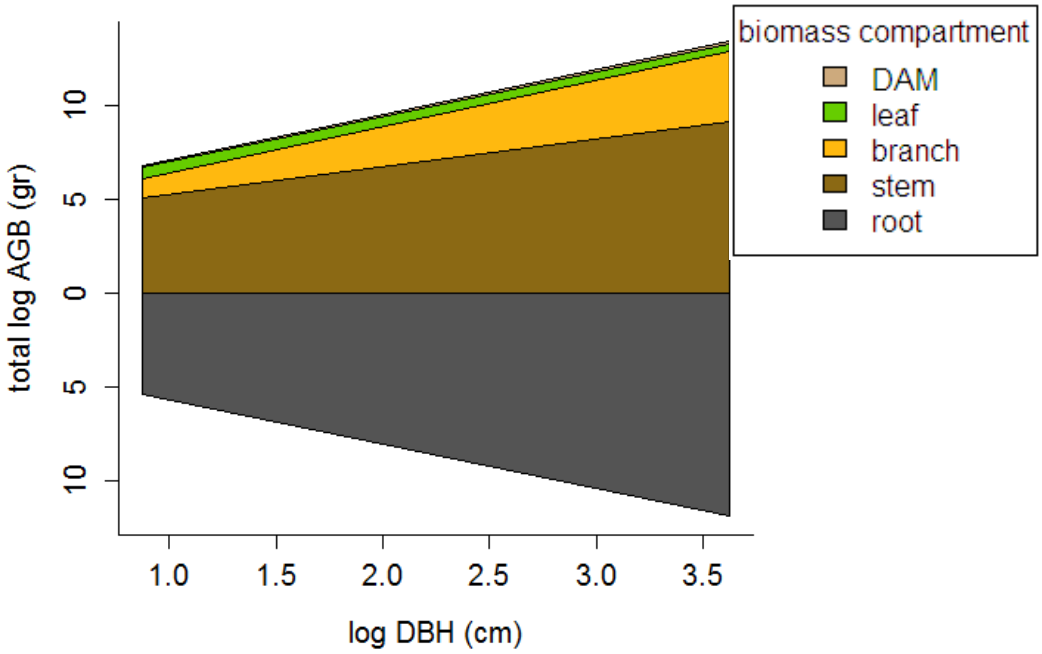


Figure 1. Above and belowground total biomass in log scale averaged among all the tree individuals in function of the log DBH. The upper line represents the total aboveground biomass; the lowest line represents the total belowground biomass. The total aboveground biomass is divided into biomass compartments. The lines represent the average real proportions of the compartment, that is, the values of those lines are not readable on the Y axis.

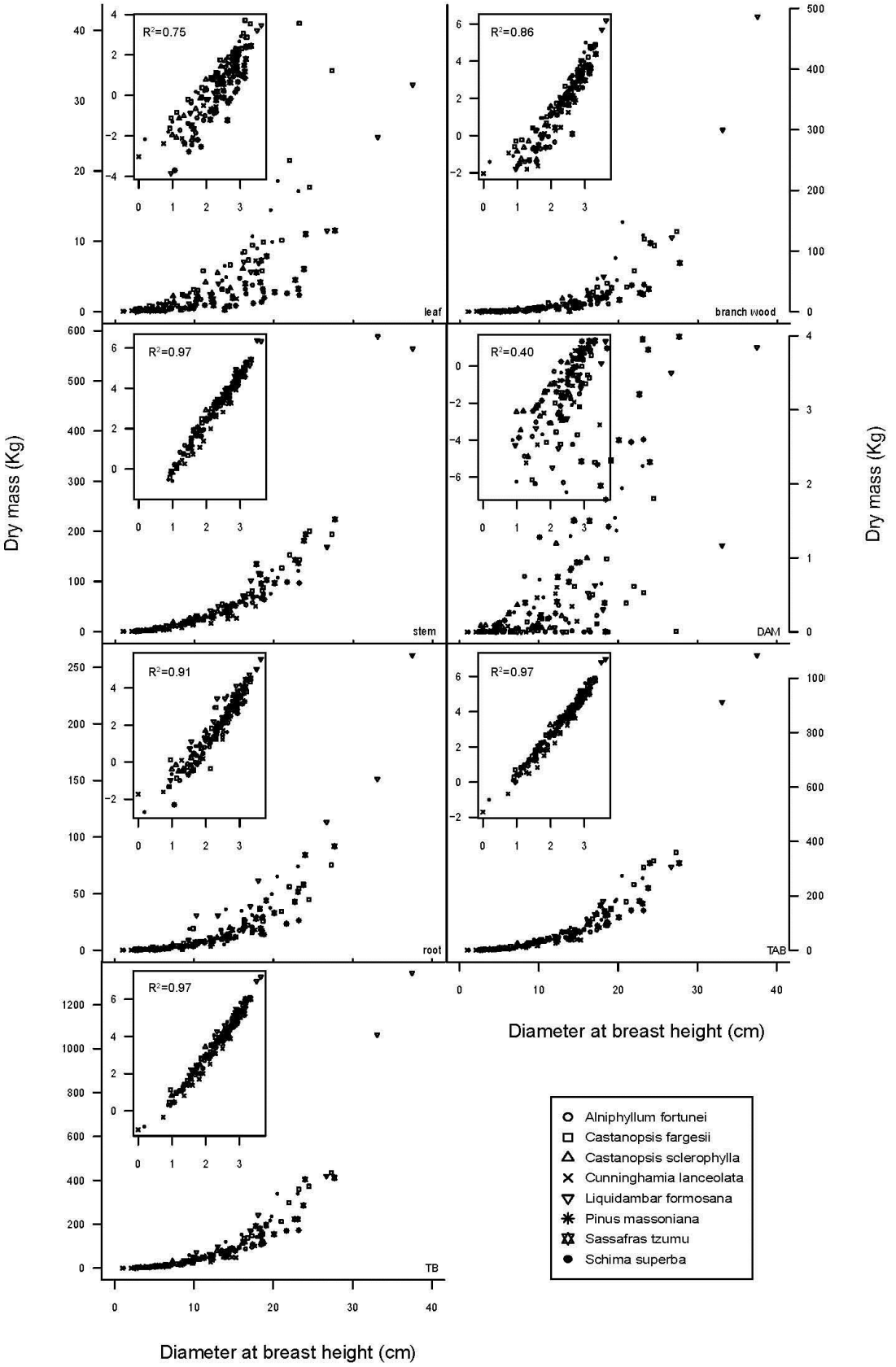


Figure 2. Biomass per tree of leaf, branch wood, stem, dead attached material (DAM), roots, total above-ground biomass (TAB) and total biomass (TB) plotted against the diameter at breast height (DBH) for the eight tree species investigated in this study. Insets display log-log relationships.

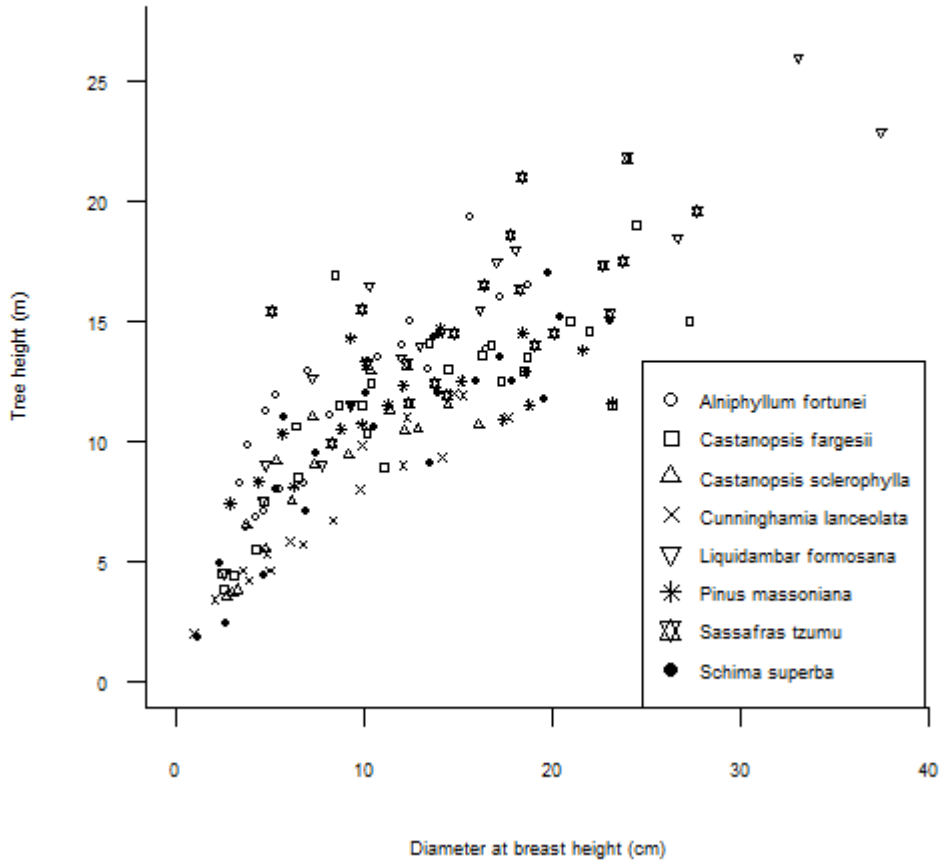


Figure 3. Tree height as a function of diameter at breast height for the eight tree species investigated in this study

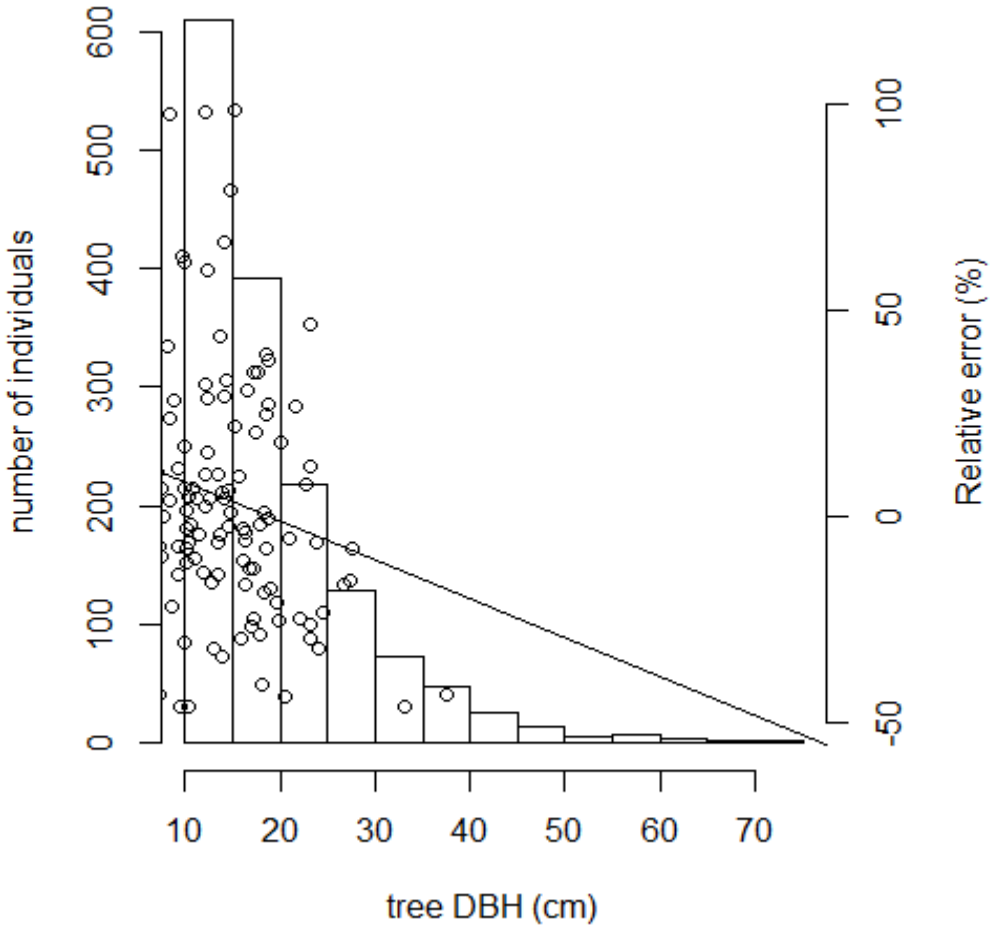


Figure 4. DBH distribution of the tree individuals bigger than 10 cm of DBH in the CSP (histogram, left y axis) and relative biomass error of the tree used to construct the allometric model (points, regressions line, right y axis). The regression line is a linear function of the relative error and tree DBH.

**Appendix**

Appendix 1: biomass raw data

| Species | DBH | Height | Crown | Leaf | Leaf sd | DAM | DAM sd | Root | Stem | Stem sd | Branch wood | AGB | AGB sd | TB |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| alf | 3.4 | 8.2 | 6.2 | 1.80E-01 | 2.08E-02 | 7.57E-03 | 2.92E-04 | 3.73E-01 | 2.30E+00 | 5.53E-02 | 2.46E-01 | 2.64E+00 | 1.76E-01 | 3.02E+00 |
| alf | 3.8 | 6.4 | 4.3 | 9.83E-02 | 2.53E-02 | 0.00E+00 | 0.00E+00 | 6.18E-01 | 2.15E+00 | 4.69E-02 | 2.67E-01 | 2.53E+00 | 6.26E-02 | 3.15E+00 |
| alf | 3.9 | 9.8 | 5.0 | 9.34E-02 | 2.69E-02 | 0.00E+00 | 0.00E+00 | 6.20E-01 | 3.23E+00 | 7.23E-02 | 2.58E-01 | 3.59E+00 | 8.26E-02 | 4.21E+00 |
| alf | 4.3 | 6.8 | 4.5 | 2.50E-01 | 5.00E-02 | 2.22E-02 | 8.58E-04 | 9.12E-01 | 2.72E+00 | 5.93E-02 | 4.86E-01 | 3.56E+00 | 1.42E-01 | 4.48E+00 |
| alf | 4.7 | 7.1 | 4.7 | 2.17E-01 | 3.36E-02 | 1.71E-03 | 6.61E-05 | 8.65E-01 | 4.21E+00 | 1.03E-01 | 4.32E-01 | 4.86E+00 | 1.61E-01 | 5.72E+00 |
| alf | 4.8 | 11.2 | 8.9 | 8.69E-02 | 2.37E-02 | 4.85E-02 | 1.87E-03 | 6.13E-01 | 4.45E+00 | 1.06E-01 | 2.39E-01 | 4.87E+00 | 1.28E-01 | 5.49E+00 |
| alf | 5.4 | 11.9 | 5.4 | 1.57E-01 | 5.27E-02 | 0.00E+00 | 0.00E+00 | 9.98E-01 | 5.23E+00 | 1.35E-01 | 4.93E-01 | 5.87E+00 | 1.62E-01 | 6.86E+00 |
| alf | 5.6 | 8.0 | 4.1 | 3.28E-01 | 6.32E-02 | 0.00E+00 | 0.00E+00 | 1.44E+00 | 5.15E+00 | 1.16E-01 | 8.70E-01 | 6.32E+00 | 1.63E-01 | 7.76E+00 |
| alf | 6.8 | 8.2 | 3.4 | 2.94E-01 | 6.87E-02 | 0.00E+00 | 0.00E+00 | 1.60E+00 | 6.95E+00 | 1.64E-01 | 9.49E-01 | 8.22E+00 | 2.06E-01 | 9.82E+00 |
| alf | 7.1 | 12.9 | 3.5 | 3.67E-01 | 4.15E-02 | 4.61E-02 | 1.78E-03 | 2.23E+00 | 1.18E+01 | 2.75E-01 | 5.44E-01 | 1.27E+01 | 3.65E-01 | 1.50E+01 |
| alf | 8.2 | 11.1 | 6.2 | 4.49E-01 | 6.10E-02 | 7.52E-01 | 2.90E-02 | 2.28E+00 | 1.22E+01 | 3.08E-01 | 7.10E-01 | 1.41E+01 | 3.73E-01 | 1.64E+01 |
| alf | 10.8 | 13.5 | 9.0 | 1.75E+00 | 2.94E-01 | 1.83E-03 | 7.05E-05 | 7.71E+00 | 2.55E+01 | 6.56E-01 | 5.22E+00 | 3.30E+01 | 9.64E-01 | 4.07E+01 |
| alf | 12.1 | 14.0 | 7.1 | 2.02E+00 | 2.65E-01 | 0.00E+00 | 0.00E+00 | 4.36E+00 | 2.88E+01 | 6.60E-01 | 7.58E+00 | 3.85E+01 | 8.97E-01 | 4.28E+01 |
| alf | 12.5 | 15.0 | 9.5 | 1.23E+00 | 2.56E-01 | 3.62E-01 | 1.40E-02 | 9.78E+00 | 3.85E+01 | 9.49E-01 | 7.99E+00 | 4.88E+01 | 1.08E+00 | 5.85E+01 |
| alf | 13.4 | 13.0 | 7.0 | 3.20E+00 | 4.30E-01 | 1.72E-01 | 6.64E-03 | 1.80E+01 | 3.52E+01 | 1.02E+00 | 8.76E+00 | 4.70E+01 | 1.30E+00 | 6.50E+01 |
| alf | 14.2 | 14.5 | 4.5 | 2.91E+00 | 4.35E-01 | 1.45E-02 | 5.58E-04 | 8.34E+00 | 3.27E+01 | 8.57E-01 | 1.32E+01 | 5.49E+01 | 1.59E+00 | 6.32E+01 |
| alf | 15.7 | 19.3 | 9.1 | 4.75E+00 | 2.93E-01 | 0.00E+00 | 0.00E+00 | 1.75E+01 | 5.94E+01 | 1.49E+00 | 1.27E+01 | 7.64E+01 | 1.69E+00 | 9.40E+01 |
| alf | 16.4 | 16.5 | 8.0 | 3.20E+00 | 5.23E-01 | 4.65E-01 | 1.79E-02 | 2.41E+01 | 7.11E+01 | 1.76E+00 | 1.92E+01 | 9.48E+01 | 2.06E+00 | 1.19E+02 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| alf | 16.5 | 13.8 | 6.9 | 2.52E+00 | 3.03E-01 | 0.00E+00 | 0.00E+00 | 2.08E+01 | 5.33E+01 | 1.38E+00 | 1.20E+01 | 6.77E+01 | 1.59E+00 | 8.85E+01 |
| alf | 17.3 | 16.0 | 9.0 | 3.78E+00 | 4.57E-01 | 2.23E-01 | 8.59E-03 | 2.06E+01 | 5.78E+01 | 1.50E+00 | 1.35E+01 | 7.48E+01 | 1.83E+00 | 9.54E+01 |
| alf | 18.7 | 16.5 | 7.2 | 2.78E+00 | 3.13E-01 | 0.00E+00 | 0.00E+00 | 3.01E+01 | 7.52E+01 | 2.01E+00 | 1.32E+01 | 9.09E+01 | 2.17E+00 | 1.21E+02 |
| caf | 2.5 | 4.5 | 0.1 | 1.96E-01 | 0.00E+00 | 0.00E+00 | 0.00E+00 | 2.65E-01 | 6.53E-01 | 1.18E-02 | 5.50E-01 | 1.33E+00 | 7.56E-02 | 1.60E+00 |
| caf | 2.6 | 3.8 | 0.9 | 3.30E-01 | 8.32E-02 | 0.00E+00 | 0.00E+00 | 1.13E+00 | 9.10E-01 | 2.11E-02 | 7.55E-01 | 1.99E+00 | 1.34E-01 | 3.11E+00 |
| caf | 3.1 | 4.4 | 1.0 | 4.32E-01 | 7.70E-02 | 0.00E+00 | 0.00E+00 | 4.21E-01 | 1.07E+00 | 2.48E-02 | 7.94E-01 | 2.27E+00 | 1.28E-01 | 2.69E+00 |
| caf | 4.3 | 5.5 | 2.0 | 8.16E-01 | 1.32E-01 | 2.14E-03 | 7.65E-05 | 7.63E-01 | 1.96E+00 | 4.48E-02 | 1.51E+00 | 4.31E+00 | 2.43E-01 | 5.08E+00 |
| caf | 4.7 | 7.5 | 1.2 | 7.38E-01 | 1.47E-01 | 0.00E+00 | 0.00E+00 | 8.57E-01 | 3.87E+00 | 7.67E-02 | 1.31E+00 | 5.87E+00 | 2.36E-01 | 6.73E+00 |
| caf | 6.4 | 10.6 | 7.6 | 9.19E-01 | 1.42E-01 | 0.00E+00 | 0.00E+00 | 2.06E+00 | 1.19E+01 | 2.40E-01 | 1.99E+00 | 1.48E+01 | 3.47E-01 | 1.68E+01 |
| caf | 6.5 | 8.5 | 6.0 | 1.46E+00 | 2.15E-01 | 1.60E-02 | 5.74E-04 | 2.15E+00 | 9.79E+00 | 2.04E-01 | 2.78E+00 | 1.40E+01 | 4.48E-01 | 1.62E+01 |
| caf | 8.5 | 16.9 | 2.9 | 2.42E+00 | 3.53E-01 | 1.36E-01 | 4.85E-03 | 7.00E-01 | 1.68E+01 | 3.80E-01 | 4.09E+00 | 2.34E+01 | 7.32E-01 | 2.41E+01 |
| caf | 8.7 | 11.5 | 4.5 | 2.24E+00 | 3.66E-01 | 2.83E-02 | 1.01E-03 | 6.20E+00 | 1.97E+01 | 4.14E-01 | 5.66E+00 | 2.77E+01 | 7.84E-01 | 3.39E+01 |
| caf | 9.9 | 11.5 | 5.0 | 3.13E+00 | 3.65E-01 | 1.47E-02 | 5.26E-04 | 1.92E+01 | 2.15E+01 | 4.73E-01 | 7.59E+00 | 3.22E+01 | 8.43E-01 | 5.14E+01 |
| caf | 10.2 | 10.3 | 6.1 | 2.67E+00 | 3.00E-01 | 6.42E-02 | 2.29E-03 | 4.79E+00 | 2.55E+01 | 5.58E-01 | 6.35E+00 | 3.46E+01 | 7.94E-01 | 3.94E+01 |
| caf | 10.4 | 12.4 | 8.3 | 3.04E+00 | 3.23E-01 | 1.80E-01 | 6.43E-03 | 5.55E+00 | 2.81E+01 | 6.42E-01 | 5.71E+00 | 3.71E+01 | 8.75E-01 | 4.26E+01 |
| caf | 11.1 | 8.9 | 3.5 | 5.81E+00 | 5.49E-01 | 1.76E-01 | 6.31E-03 | 7.75E+00 | 2.36E+01 | 4.84E-01 | 1.44E+01 | 4.39E+01 | 1.13E+00 | 5.17E+01 |
| caf | 13.5 | 14.1 | 8.7 | 3.17E+00 | 3.87E-01 | 0.00E+00 | 0.00E+00 | 9.87E+00 | 5.45E+01 | 1.66E+00 | 1.02E+01 | 6.78E+01 | 1.81E+00 | 7.77E+01 |
| caf | 14.5 | 13.0 | 5.5 | 6.65E+00 | 6.62E-01 | 6.12E-01 | 2.19E-02 | 1.25E+01 | 5.07E+01 | 1.09E+00 | 1.76E+01 | 7.56E+01 | 1.67E+00 | 8.81E+01 |
| caf | 16.3 | 13.6 | 6.5 | 8.51E+00 | 6.73E-01 | 2.44E-02 | 8.72E-04 | 2.69E+01 | 7.06E+01 | 1.39E+00 | 2.87E+01 | 1.08E+02 | 1.97E+00 | 1.35E+02 |
| caf | 16.8 | 14.0 | 5.5 | 7.34E+00 | 9.03E-01 | 5.02E-01 | 1.79E-02 | 2.23E+01 | 7.55E+01 | 1.54E+00 | 3.22E+01 | 1.16E+02 | 2.38E+00 | 1.38E+02 |
| caf | 17.3 | 12.5 | 6.0 | 9.46E+00 | 9.05E-01 | 1.11E-01 | 3.96E-03 | 1.59E+01 | 8.14E+01 | 1.69E+00 | 4.04E+01 | 1.32E+02 | 2.52E+00 | 1.47E+02 |
| caf | 18.6 | 12.9 | 4.4 | 5.79E+00 | 1.02E+00 | 9.87E-01 | 3.53E-02 | 2.85E+01 | 8.17E+01 | 1.73E+00 | 4.71E+01 | 1.36E+02 | 2.97E+00 | 1.64E+02 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| caf | 18.7 | 13.5 | 7.0 | 9.87E+00 | 9.93E-01 | 0.00E+00 | 0.00E+00 | 2.58E+01 | 8.77E+01 | 2.03E+00 | 3.19E+01 | 1.29E+02 | 2.77E+00 | 1.55E+02 |
| caf | 21.0 | 15.0 | 6.5 | 1.01E+01 | 1.04E+00 | 3.91E-01 | 1.40E-02 | 3.44E+01 | 1.27E+02 | 2.87E+00 | 4.11E+01 | 1.78E+02 | 3.65E+00 | 2.13E+02 |
| caf | 22.0 | 14.6 | 5.4 | 2.15E+01 | 1.71E+00 | 6.16E-01 | 2.20E-02 | 5.62E+01 | 1.53E+02 | 2.90E+00 | 6.76E+01 | 2.42E+02 | 4.34E+00 | 2.98E+02 |
| caf | 23.2 | 11.5 | 3.5 | 4.10E+01 | 2.66E+00 | 5.32E-01 | 1.90E-02 | 5.48E+01 | 1.44E+02 | 2.63E+00 | 1.20E+02 | 3.05E+02 | 5.84E+00 | 3.59E+02 |
| caf | 24.5 | 19.0 | 6.2 | 1.77E+01 | 1.59E+00 | 1.80E+00 | 6.45E-02 | 4.47E+01 | 2.00E+02 | 3.80E+00 | 1.09E+02 | 3.29E+02 | 5.28E+00 | 3.73E+02 |
| caf | 27.3 | 15.0 | 5.0 | 3.43E+01 | 2.73E+00 | 5.48E-03 | 1.96E-04 | 7.54E+01 | 1.94E+02 | 3.86E+00 | 1.32E+02 | 3.60E+02 | 6.55E+00 | 4.35E+02 |
| cas | 2.7 | 3.5 | 1.0 | 1.42E-01 | 0.00E+00 | 8.41E-02 | 4.32E-03 | 6.81E-01 | 8.27E-01 | 1.93E-02 | 4.27E-01 | 1.58E+00 | 9.11E-02 | 2.26E+00 |
| cas | 3.1 | 3.7 | 1.1 | 1.23E-01 | 0.00E+00 | 3.09E-02 | 1.59E-03 | 8.63E-01 | 1.01E+00 | 2.16E-02 | 2.87E-01 | 1.66E+00 | 8.88E-02 | 2.53E+00 |
| cas | 3.3 | 3.8 | 1.8 | 3.19E-01 | 6.38E-02 | 8.77E-02 | 4.50E-03 | 6.11E-01 | 1.31E+00 | 3.03E-02 | 5.29E-01 | 2.22E+00 | 1.14E-01 | 2.83E+00 |
| cas | 3.8 | 6.5 | 3.5 | 3.62E-01 | 7.62E-02 | 7.43E-03 | 3.81E-04 | 6.95E-01 | 2.08E+00 | 5.15E-02 | 7.40E-01 | 3.16E+00 | 1.48E-01 | 3.85E+00 |
| cas | 4.8 | 5.5 | 2.0 | 1.10E-01 | 0.00E+00 | 1.03E-01 | 5.29E-03 | 1.25E+00 | 3.29E+00 | 7.54E-02 | 2.74E-01 | 4.13E+00 | 1.35E-01 | 5.38E+00 |
| cas | 5.4 | 9.2 | 4.5 | 5.18E-01 | 9.91E-02 | 6.67E-02 | 3.42E-03 | 1.52E+00 | 5.72E+00 | 1.42E-01 | 1.04E+00 | 7.32E+00 | 2.33E-01 | 8.84E+00 |
| cas | 6.2 | 7.5 | 4.0 | 8.70E-01 | 1.35E-01 | 2.37E-01 | 1.22E-02 | 2.55E+00 | 6.63E+00 | 1.90E-01 | 1.77E+00 | 9.50E+00 | 3.16E-01 | 1.21E+01 |
| cas | 7.3 | 11.0 | 6.0 | 2.20E+00 | 3.05E-01 | 3.63E-01 | 1.86E-02 | 5.39E+00 | 1.84E+01 | 3.83E-01 | 4.80E+00 | 2.58E+01 | 7.11E-01 | 3.11E+01 |
| cas | 7.4 | 9.0 | 3.0 | 1.39E+00 | 2.83E-01 | 4.59E-02 | 2.35E-03 | 3.36E+00 | 1.20E+01 | 2.88E-01 | 3.42E+00 | 1.68E+01 | 6.67E-01 | 2.02E+01 |
| cas | 9.2 | 9.4 | 4.5 | 2.09E+00 | 3.23E-01 | 7.84E-02 | 4.02E-03 | 3.89E+00 | 1.57E+01 | 4.16E-01 | 5.20E+00 | 2.30E+01 | 7.31E-01 | 2.69E+01 |
| cas | 10.4 | 12.9 | 4.0 | 2.37E+00 | 2.74E-01 | 5.19E-02 | 2.66E-03 | 6.47E+00 | 2.19E+01 | 5.20E-01 | 7.24E+00 | 3.16E+01 | 7.31E-01 | 3.81E+01 |
| cas | 11.4 | 11.3 | 4.0 | 4.17E+00 | 4.52E-01 | 5.38E-02 | 2.76E-03 | 7.77E+00 | 3.02E+01 | 7.48E-01 | 9.46E+00 | 4.39E+01 | 1.11E+00 | 5.17E+01 |
| cas | 12.2 | 10.4 | 2.9 | 2.61E+00 | 4.71E-01 | 1.20E+00 | 6.13E-02 | 1.04E+01 | 3.30E+01 | 8.71E-01 | 9.11E+00 | 4.59E+01 | 1.23E+00 | 5.63E+01 |
| cas | 12.9 | 10.5 | 3.0 | 5.50E+00 | 8.61E-01 | 2.16E-01 | 1.11E-02 | 1.12E+01 | 3.98E+01 | 9.03E-01 | 2.15E+01 | 6.70E+01 | 1.98E+00 | 7.83E+01 |
| cas | 14.5 | 11.5 | 4.4 | 3.33E+00 | 4.91E-01 | 1.51E+00 | 7.76E-02 | 1.98E+01 | 4.16E+01 | 9.98E-01 | 1.45E+01 | 6.09E+01 | 1.42E+00 | 8.07E+01 |
| cas | 16.1 | 10.7 | 4.9 | 6.10E+00 | 7.23E-01 | 9.95E-01 | 5.11E-02 | 1.95E+01 | 5.94E+01 | 1.39E+00 | 2.65E+01 | 9.30E+01 | 2.02E+00 | 1.13E+02 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| cul | 1.0 | 2.0 | 1.5 | 4.89E-02 | 1.41E-02 | 0.00E+00 | 0.00E+00 | 1.77E-01 | 0.00E+00 | 0.00E+00 | 1.31E-01 | 1.83E-01 | 2.33E-02 | 3.60E-01 |
| cul | 2.1 | 3.4 | 3.0 | 9.21E-02 | 3.58E-02 | 0.00E+00 | 0.00E+00 | 2.00E-01 | 0.00E+00 | 0.00E+00 | 3.93E-01 | 5.13E-01 | 7.04E-02 | 7.14E-01 |
| cul | 3.6 | 4.6 | 3.5 | 1.20E-01 | 0.00E+00 | 5.32E-03 | 5.81E-04 | 1.11E+00 | 1.53E+00 | 4.32E-02 | 1.65E-01 | 1.75E+00 | 5.62E-02 | 2.85E+00 |
| cul | 3.9 | 4.2 | 2.7 | 8.87E-02 | 0.00E+00 | 0.00E+00 | 0.00E+00 | 6.43E-01 | 1.29E+00 | 4.44E-02 | 2.79E-01 | 1.61E+00 | 6.15E-02 | 2.25E+00 |
| cul | 4.9 | 5.3 | 4.1 | 2.10E-01 | 5.06E-02 | 1.12E-01 | 1.22E-02 | 8.81E-01 | 2.46E+00 | 7.41E-02 | 4.95E-01 | 3.27E+00 | 1.46E-01 | 4.15E+00 |
| cul | 5.0 | 4.6 | 3.7 | 1.26E-01 | 0.00E+00 | 1.42E-02 | 1.55E-03 | 1.65E+00 | 2.06E+00 | 6.71E-02 | 1.96E-01 | 2.30E+00 | 8.27E-02 | 3.95E+00 |
| cul | 6.1 | 5.8 | 3.2 | 4.05E-01 | 8.69E-02 | 7.87E-02 | 8.60E-03 | 1.01E+00 | 2.92E+00 | 1.19E-01 | 1.11E+00 | 4.47E+00 | 2.42E-01 | 5.48E+00 |
| cul | 6.8 | 5.7 | 3.0 | 6.09E-01 | 1.08E-01 | 0.00E+00 | 0.00E+00 | 1.20E+00 | 4.01E+00 | 1.45E-01 | 1.67E+00 | 6.31E+00 | 2.58E-01 | 7.51E+00 |
| cul | 8.4 | 6.7 | 4.6 | 5.08E-01 | 1.17E-01 | 0.00E+00 | 0.00E+00 | 3.21E+00 | 7.31E+00 | 2.55E-01 | 1.33E+00 | 9.14E+00 | 3.64E-01 | 1.24E+01 |
| cul | 9.8 | 8.0 | 4.6 | 5.68E-01 | 1.18E-01 | 4.63E-01 | 5.06E-02 | 5.55E+00 | 1.32E+01 | 4.35E-01 | 1.54E+00 | 1.58E+01 | 5.28E-01 | 2.14E+01 |
| cul | 9.9 | 9.8 | 5.4 | 5.70E-01 | 1.28E-01 | 8.38E-02 | 9.15E-03 | 5.17E+00 | 1.47E+01 | 4.67E-01 | 1.57E+00 | 1.69E+01 | 5.67E-01 | 2.21E+01 |
| cul | 12.1 | 9.0 | 2.5 | 1.32E+00 | 2.73E-01 | 5.18E-01 | 5.66E-02 | 3.41E+00 | 1.67E+01 | 5.83E-01 | 6.62E+00 | 2.51E+01 | 8.45E-01 | 2.86E+01 |
| cul | 12.3 | 11.0 | 4.0 | 1.27E+00 | 2.62E-01 | 6.03E-01 | 6.58E-02 | 5.57E+00 | 2.59E+01 | 8.80E-01 | 3.51E+00 | 3.12E+01 | 1.09E+00 | 3.68E+01 |
| cul | 14.2 | 9.3 | 5.5 | 2.98E+00 | 4.71E-01 | 3.45E-01 | 3.77E-02 | 1.16E+01 | 2.55E+01 | 9.66E-01 | 8.64E+00 | 3.74E+01 | 1.44E+00 | 4.91E+01 |
| cul | 14.8 | 12.0 | 5.5 | 2.27E+00 | 3.90E-01 | 1.43E-01 | 1.57E-02 | 1.05E+01 | 3.15E+01 | 1.20E+00 | 5.89E+00 | 3.97E+01 | 1.49E+00 | 5.02E+01 |
| cul | 15.3 | 11.9 | 4.2 | 1.84E+00 | 3.18E-01 | 2.30E+00 | 2.51E-01 | 1.17E+01 | 2.64E+01 | 1.17E+00 | 6.73E+00 | 3.72E+01 | 1.42E+00 | 4.89E+01 |
| cul | 17.7 | 11.0 | 4.1 | 7.25E+00 | 8.02E-01 | 2.80E+00 | 3.05E-01 | 1.81E+01 | 5.05E+01 | 1.74E+00 | 2.23E+01 | 8.25E+01 | 2.40E+00 | 1.01E+02 |
| lif | 2.6 | 4.5 | 2.3 | 2.13E-02 | 0.00E+00 | 1.38E-02 | 4.37E-04 | 3.83E-01 | 7.89E-01 | 2.06E-02 | 1.68E-01 | 1.01E+00 | 3.82E-02 | 1.39E+00 |
| lif | 4.6 | 7.5 | 2.5 | 4.18E-01 | 1.03E-01 | 0.00E+00 | 0.00E+00 | 2.07E+00 | 2.99E+00 | 8.16E-02 | 1.39E+00 | 4.71E+00 | 3.43E-01 | 6.78E+00 |
| lif | 4.8 | 9.0 | 6.0 | 2.38E-01 | 0.00E+00 | 3.45E-02 | 1.09E-03 | 3.05E+00 | 4.63E+00 | 1.06E-01 | 1.34E+00 | 6.25E+00 | 1.93E-01 | 9.30E+00 |
| lif | 7.3 | 12.6 | 7.4 | 8.32E-01 | 1.15E-01 | 0.00E+00 | 0.00E+00 | 3.27E+00 | 1.21E+01 | 2.83E-01 | 3.01E+00 | 1.58E+01 | 4.34E-01 | 1.91E+01 |
| lif | 7.8 | 9.0 | 4.1 | 8.44E-01 | 1.56E-01 | 4.10E-03 | 1.30E-04 | 4.29E+00 | 1.20E+01 | 2.90E-01 | 3.44E+00 | 1.63E+01 | 5.43E-01 | 2.06E+01 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| lif | 9.3 | 11.5 | 5.5 | 1.15E+00 | 2.23E-01 | 1.15E-02 | 3.65E-04 | 8.98E+00 | 2.12E+01 | 4.87E-01 | 4.64E+00 | 2.70E+01 | 7.61E-01 | 3.60E+01 |
| lif | 10.3 | 16.5 | 4.6 | 1.77E+00 | 2.77E-01 | 2.43E-01 | 7.72E-03 | 3.09E+01 | 3.24E+01 | 8.41E-01 | 6.64E+00 | 4.13E+01 | 1.15E+00 | 7.23E+01 |
| lif | 12.0 | 13.5 | 5.5 | 2.46E+00 | 3.33E-01 | 5.93E-02 | 1.88E-03 | 1.13E+01 | 4.16E+01 | 9.49E-01 | 8.85E+00 | 5.31E+01 | 1.29E+00 | 6.44E+01 |
| lif | 13.0 | 14.0 | 6.0 | 4.01E+00 | 5.92E-01 | 0.00E+00 | 0.00E+00 | 3.08E+01 | 5.06E+01 | 1.15E+00 | 1.32E+01 | 6.77E+01 | 2.21E+00 | 9.85E+01 |
| lif | 16.2 | 15.5 | 4.0 | 7.06E+00 | 9.77E-01 | 5.27E-01 | 1.67E-02 | 1.76E+01 | 6.84E+01 | 1.67E+00 | 3.11E+01 | 1.07E+02 | 2.82E+00 | 1.24E+02 |
| lif | 17.1 | 17.5 | 5.0 | 5.63E+00 | 6.89E-01 | 6.30E-01 | 2.00E-02 | 3.88E+01 | 1.02E+02 | 2.39E+00 | 2.46E+01 | 1.32E+02 | 2.98E+00 | 1.71E+02 |
| lif | 18.1 | 18.0 | 7.0 | 6.87E+00 | 1.18E+00 | 3.02E-01 | 9.59E-03 | 6.15E+01 | 1.16E+02 | 2.76E+00 | 5.80E+01 | 1.80E+02 | 4.34E+00 | 2.42E+02 |
| lif | 26.7 | 18.5 | 3.0 | 1.15E+01 | 1.55E+00 | 3.50E+00 | 1.11E-01 | 1.13E+02 | 1.69E+02 | 4.76E+00 | 1.22E+02 | 3.06E+02 | 7.15E+00 | 4.20E+02 |
| lif | 33.1 | 26.0 | 5.8 | 2.48E+01 | 3.22E+00 | 1.17E+00 | 3.71E-02 | 1.51E+02 | 5.89E+02 | 1.29E+01 | 3.00E+02 | 9.12E+02 | 1.70E+01 | 1.06E+03 |
| lif | 37.5 | 22.9 | 4.6 | 3.23E+01 | 3.92E+00 | 3.84E+00 | 1.22E-01 | 2.61E+02 | 5.65E+02 | 1.30E+01 | 4.87E+02 | 1.08E+03 | 1.94E+01 | 1.35E+03 |
| pim | 2.9 | 7.4 | 5.0 | 2.47E-02 | 9.48E-03 | 2.08E-02 | 6.01E-04 | 1.00E-01 | 1.23E+00 | 2.47E-02 | 2.21E-01 | 1.50E+00 | 3.65E-02 | 1.60E+00 |
| pim | 4.4 | 8.3 | 5.6 | 6.26E-02 | 2.15E-02 | 8.85E-02 | 2.56E-03 | 5.10E-01 | 2.92E+00 | 6.25E-02 | 5.20E-01 | 3.55E+00 | 1.22E-01 | 4.06E+00 |
| pim | 5.7 | 10.3 | 7.7 | 1.11E-01 | 0.00E+00 | 1.55E-01 | 4.47E-03 | 9.05E-01 | 7.94E+00 | 1.63E-01 | 9.65E-01 | 9.25E+00 | 2.44E-01 | 1.02E+01 |
| pim | 6.3 | 8.1 | 6.0 | 7.91E-02 | 0.00E+00 | 2.58E-01 | 7.47E-03 | 1.28E+00 | 5.09E+00 | 1.33E-01 | 5.29E-01 | 6.16E+00 | 2.06E-01 | 7.44E+00 |
| pim | 8.8 | 10.5 | 6.6 | 5.11E-01 | 1.28E-01 | 2.49E-01 | 7.18E-03 | 3.43E+00 | 1.43E+01 | 3.25E-01 | 3.05E+00 | 1.78E+01 | 4.94E-01 | 2.12E+01 |
| pim | 9.3 | 14.3 | 7.8 | 4.16E-01 | 1.04E-01 | 7.39E-02 | 2.13E-03 | 3.85E+00 | 2.46E+01 | 4.95E-01 | 4.43E+00 | 2.95E+01 | 6.17E-01 | 3.33E+01 |
| pim | 9.9 | 10.7 | 5.0 | 4.45E-01 | 1.35E-01 | 1.16E-01 | 3.34E-03 | 4.22E+00 | 2.04E+01 | 4.28E-01 | 5.30E+00 | 2.62E+01 | 6.65E-01 | 3.04E+01 |
| pim | 10.1 | 13.3 | 8.5 | 9.24E-01 | 1.42E-01 | 1.28E+00 | 3.70E-02 | 5.70E+00 | 2.64E+01 | 5.47E-01 | 6.41E+00 | 3.48E+01 | 7.61E-01 | 4.05E+01 |
| pim | 11.3 | 11.5 | 6.5 | 9.23E-01 | 2.06E-01 | 1.89E-01 | 5.47E-03 | 6.77E+00 | 2.95E+01 | 6.19E-01 | 8.99E+00 | 3.95E+01 | 9.56E-01 | 4.62E+01 |
| pim | 12.1 | 12.3 | 4.5 | 2.03E+00 | 2.38E-01 | 2.50E-01 | 7.22E-03 | 8.47E+00 | 3.07E+01 | 6.62E-01 | 1.07E+01 | 4.29E+01 | 1.06E+00 | 5.14E+01 |
| pim | 14.0 | 14.5 | 6.0 | 7.25E-01 | 2.40E-01 | 8.35E-01 | 2.41E-02 | 1.20E+01 | 4.43E+01 | 9.27E-01 | 1.71E+01 | 6.29E+01 | 1.49E+00 | 7.49E+01 |
| pim | 14.1 | 14.7 | 8.8 | 6.93E-01 | 1.88E-01 | 8.59E-01 | 2.48E-02 | 1.37E+01 | 4.55E+01 | 9.21E-01 | 1.62E+01 | 6.32E+01 | 1.28E+00 | 7.70E+01 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pim | 15.2 | 12.5 | 7.0 | 8.48E-01 | 2.11E-01 | 9.40E-01 | 2.72E-02 | 1.19E+01 | 5.15E+01 | 1.08E+00 | 1.34E+01 | 6.67E+01 | 1.43E+00 | 7.86E+01 |
| pim | 17.4 | 10.9 | 5.6 | 1.18E+00 | 3.41E-01 | 2.26E+00 | 6.54E-02 | 1.75E+01 | 6.87E+01 | 1.72E+00 | 1.84E+01 | 9.11E+01 | 2.18E+00 | 1.09E+02 |
| pim | 18.5 | 14.5 | 5.7 | 1.37E+00 | 3.62E-01 | 1.79E+00 | 5.17E-02 | 1.44E+01 | 6.68E+01 | 1.40E+00 | 2.27E+01 | 9.29E+01 | 2.06E+00 | 1.07E+02 |
| pim | 18.6 | 12.9 | 6.1 | 3.23E+00 | 4.42E-01 | 3.83E+00 | 1.11E-01 | 1.73E+01 | 6.67E+01 | 1.60E+00 | 3.14E+01 | 1.05E+02 | 2.58E+00 | 1.22E+02 |
| pim | 18.8 | 11.5 | 6.0 | 1.95E+00 | 4.40E-01 | 1.42E+00 | 4.10E-02 | 1.41E+01 | 6.41E+01 | 1.36E+00 | 3.16E+01 | 9.90E+01 | 2.25E+00 | 1.13E+02 |
| pim | 21.7 | 13.8 | 6.5 | 2.58E+00 | 4.99E-01 | 2.56E+00 | 7.41E-02 | 2.35E+01 | 9.87E+01 | 2.17E+00 | 4.35E+01 | 1.47E+02 | 3.29E+00 | 1.70E+02 |
| pim | 23.2 | 11.6 | 5.4 | 2.36E+00 | 5.03E-01 | 2.60E+00 | 7.51E-02 | 2.64E+01 | 9.68E+01 | 2.55E+00 | 4.45E+01 | 1.46E+02 | 3.58E+00 | 1.73E+02 |
| sat | 5.1 | 15.4 | 10.9 | 1.93E-01 | 3.97E-02 | 1.19E-01 | 2.80E-03 | 6.55E-01 | 6.73E+00 | 1.85E-01 | 5.99E-01 | 7.63E+00 | 2.28E-01 | 8.28E+00 |
| sat | 8.3 | 9.9 | 6.8 | 3.01E-01 | 6.62E-02 | 3.95E-01 | 9.29E-03 | 3.00E+00 | 1.39E+01 | 3.96E-01 | 1.54E+00 | 1.62E+01 | 4.68E-01 | 1.92E+01 |
| sat | 9.9 | 15.5 | 10.5 | 7.95E-01 | 1.42E-01 | 6.17E-02 | 1.45E-03 | 3.57E+00 | 2.51E+01 | 6.18E-01 | 3.81E+00 | 2.98E+01 | 7.78E-01 | 3.33E+01 |
| sat | 10.2 | 13.2 | 7.5 | 1.21E+00 | 2.42E-01 | 1.98E-01 | 4.67E-03 | 7.12E+00 | 2.80E+01 | 6.54E-01 | 6.45E+00 | 3.59E+01 | 1.06E+00 | 4.30E+01 |
| sat | 12.3 | 13.2 | 7.5 | 1.76E+00 | 2.20E-01 | 4.09E-01 | 9.63E-03 | 8.92E+00 | 3.21E+01 | 7.45E-01 | 7.69E+00 | 4.19E+01 | 1.05E+00 | 5.08E+01 |
| sat | 12.4 | 11.6 | 7.6 | 8.86E-01 | 1.35E-01 | 7.42E-01 | 1.75E-02 | 8.49E+00 | 3.12E+01 | 7.11E-01 | 5.24E+00 | 3.81E+01 | 8.52E-01 | 4.66E+01 |
| sat | 13.8 | 12.4 | 7.7 | 2.95E-01 | 5.34E-02 | 6.75E-01 | 1.59E-02 | 1.16E+01 | 3.96E+01 | 1.01E+00 | 1.09E+00 | 4.16E+01 | 1.05E+00 | 5.32E+01 |
| sat | 14.4 | 11.9 | 6.5 | 7.64E-01 | 1.60E-01 | 1.50E+00 | 3.53E-02 | 1.41E+01 | 3.97E+01 | 9.34E-01 | 7.27E+00 | 4.93E+01 | 1.12E+00 | 6.34E+01 |
| sat | 14.8 | 14.5 | 6.4 | 1.91E+00 | 2.79E-01 | 9.39E-01 | 2.21E-02 | 1.80E+01 | 5.39E+01 | 1.27E+00 | 1.44E+01 | 7.11E+01 | 1.64E+00 | 8.92E+01 |
| sat | 16.4 | 16.5 | 6.3 | 4.00E+00 | 4.19E-01 | 1.50E+00 | 3.53E-02 | 2.52E+01 | 6.90E+01 | 1.64E+00 | 2.11E+01 | 9.56E+01 | 2.30E+00 | 1.21E+02 |
| sat | 17.8 | 18.6 | 10.4 | 5.58E+00 | 4.11E-01 | 1.97E+00 | 4.65E-02 | 2.80E+01 | 1.35E+02 | 2.72E+00 | 2.24E+01 | 1.65E+02 | 3.11E+00 | 1.93E+02 |
| sat | 18.3 | 16.3 | 5.9 | 4.18E+00 | 5.07E-01 | 3.92E-01 | 9.23E-03 | 3.66E+01 | 1.14E+02 | 2.40E+00 | 2.53E+01 | 1.43E+02 | 3.00E+00 | 1.80E+02 |
| sat | 18.4 | 21.0 | 11.2 | 7.27E+00 | 4.67E-01 | 5.76E-03 | 1.35E-04 | 1.93E+01 | 9.60E+01 | 2.33E+00 | 2.43E+01 | 1.28E+02 | 2.83E+00 | 1.47E+02 |
| sat | 19.1 | 14.0 | 9.0 | 7.86E+00 | 5.47E-01 | 2.32E+00 | 5.45E-02 | 4.40E+01 | 1.03E+02 | 2.19E+00 | 3.92E+01 | 1.52E+02 | 2.99E+00 | 1.96E+02 |
| sat | 20.1 | 14.5 | 6.2 | 2.77E+00 | 3.67E-01 | 2.59E+00 | 6.10E-02 | 3.30E+01 | 9.65E+01 | 2.44E+00 | 1.94E+01 | 1.21E+02 | 2.85E+00 | 1.54E+02 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| sat | 22.7 | 17.3 | 9.1 | 4.48E+00 | 5.40E-01 | 3.21E+00 | 7.55E-02 | 4.28E+01 | 1.43E+02 | 3.23E+00 | 3.09E+01 | 1.81E+02 | 3.84E+00 | 2.24E+02 |
| sat | 23.1 | 15.3 | 8.9 | 3.23E+00 | 4.77E-01 | 3.95E+00 | 9.30E-02 | 5.16E+01 | 1.36E+02 | 3.24E+00 | 2.87E+01 | 1.72E+02 | 3.75E+00 | 2.24E+02 |
| sat | 23.8 | 17.5 | 9.9 | 6.06E+00 | 5.80E-01 | 3.81E+00 | 8.97E-02 | 5.80E+01 | 1.81E+02 | 3.96E+00 | 3.76E+01 | 2.28E+02 | 4.52E+00 | 2.86E+02 |
| sat | 24.0 | 21.8 | 6.6 | 1.10E+01 | 1.41E+00 | 2.29E+00 | 5.39E-02 | 8.43E+01 | 1.94E+02 | 4.42E+00 | 1.13E+02 | 3.20E+02 | 7.12E+00 | 4.04E+02 |
| sat | 27.7 | 19.6 | 9.2 | 1.16E+01 | 9.79E-01 | 3.99E+00 | 9.38E-02 | 9.19E+01 | 2.24E+02 | 5.06E+00 | 8.05E+01 | 3.20E+02 | 6.43E+00 | 4.12E+02 |
| scs | 1.2 | 1.8 | 0.4 | 1.16E-01 | 1.71E-02 | 0.00E+00 | 0.00E+00 | 6.80E-02 | 0.00E+00 | 0.00E+00 | 2.44E-01 | 3.65E-01 | 5.49E-02 | 4.33E-01 |
| scs | 2.4 | 4.9 | 1.6 | 1.65E-01 | 2.57E-02 | 1.83E-02 | 2.92E-04 | 2.62E-01 | 5.88E-01 | 1.23E-02 | 3.38E-01 | 1.10E+00 | 7.78E-02 | 1.36E+00 |
| scs | 2.7 | 2.4 | 1.3 | 2.73E-01 | 0.00E+00 | 1.90E-03 | 3.04E-05 | 5.20E-01 | 5.54E-01 | 1.05E-02 | 2.04E-01 | 1.02E+00 | 6.48E-02 | 1.54E+00 |
| scs | 4.7 | 4.4 | 1.7 | 6.69E-01 | 9.14E-02 | 1.08E-01 | 1.72E-03 | 1.37E+00 | 2.81E+00 | 4.63E-02 | 1.27E+00 | 4.81E+00 | 2.52E-01 | 6.18E+00 |
| scs | 5.4 | 8.0 | 0.9 | 1.20E+00 | 1.47E-01 | 0.00E+00 | 0.00E+00 | 2.36E+00 | 5.91E+00 | 8.39E-02 | 2.58E+00 | 9.67E+00 | 4.07E-01 | 1.20E+01 |
| scs | 5.8 | 11.0 | 2.0 | 1.14E+00 | 1.55E-01 | 2.50E-02 | 3.99E-04 | 2.39E+00 | 6.19E+00 | 9.39E-02 | 2.61E+00 | 9.91E+00 | 4.31E-01 | 1.23E+01 |
| scs | 6.9 | 7.1 | 2.3 | 1.24E+00 | 1.45E-01 | 2.65E-01 | 4.24E-03 | 3.89E+00 | 7.25E+00 | 1.07E-01 | 4.35E+00 | 1.30E+01 | 4.16E-01 | 1.69E+01 |
| scs | 7.5 | 9.5 | 2.2 | 1.28E+00 | 1.51E-01 | 4.81E-02 | 7.68E-04 | 3.18E+00 | 1.03E+01 | 1.70E-01 | 2.87E+00 | 1.45E+01 | 4.94E-01 | 1.77E+01 |
| scs | 9.4 | 11.5 | 5.5 | 2.68E+00 | 3.01E-01 | 3.29E-01 | 5.25E-03 | 1.90E+01 | 2.89E+01 | 4.34E-01 | 8.17E+00 | 3.99E+01 | 9.36E-01 | 5.89E+01 |
| scs | 10.1 | 12.0 | 5.5 | 1.63E+00 | 1.87E-01 | 7.07E-01 | 1.13E-02 | 6.86E+00 | 2.41E+01 | 4.20E-01 | 3.46E+00 | 2.99E+01 | 6.91E-01 | 3.68E+01 |
| scs | 10.6 | 10.6 | 4.4 | 2.01E+00 | 2.02E-01 | 4.67E-01 | 7.46E-03 | 8.56E+00 | 2.43E+01 | 3.80E-01 | 7.42E+00 | 3.41E+01 | 6.99E-01 | 4.26E+01 |
| scs | 13.5 | 9.1 | 2.0 | 4.43E+00 | 4.27E-01 | 1.89E+00 | 3.02E-02 | 1.48E+01 | 5.03E+01 | 7.42E-01 | 1.33E+01 | 6.99E+01 | 1.27E+00 | 8.47E+01 |
| scs | 13.8 | 14.3 | 3.0 | 6.50E+00 | 6.12E-01 | 1.22E-01 | 1.95E-03 | 5.07E+00 | 4.22E+01 | 5.80E-01 | 2.63E+01 | 7.50E+01 | 1.67E+00 | 8.00E+01 |
| scs | 14.0 | 12.0 | 3.5 | 4.91E+00 | 5.25E-01 | 1.29E+00 | 2.07E-02 | 3.62E+01 | 5.35E+01 | 7.37E-01 | 2.47E+01 | 8.37E+01 | 1.68E+00 | 1.20E+02 |
| scs | 16.0 | 12.5 | 4.5 | 8.32E+00 | 9.14E-01 | 1.01E+00 | 1.61E-02 | 3.48E+01 | 7.30E+01 | 1.10E+00 | 3.65E+01 | 1.18E+02 | 2.71E+00 | 1.53E+02 |
| scs | 17.3 | 13.5 | 3.0 | 1.07E+01 | 1.11E+00 | 1.11E-01 | 1.77E-03 | 3.13E+01 | 7.57E+01 | 1.13E+00 | 5.45E+01 | 1.40E+02 | 3.24E+00 | 1.72E+02 |
| scs | 17.9 | 12.5 | 5.5 | 9.00E+00 | 8.17E-01 | 6.53E-01 | 1.04E-02 | 3.02E+01 | 6.99E+01 | 1.06E+00 | 3.27E+01 | 1.12E+02 | 2.48E+00 | 1.42E+02 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| scs | 19.6 | 11.7 | 2.3 | 1.44E+01 | 1.34E+00 | 1.54E+00 | 2.46E-02 | 3.74E+01 | 7.55E+01 | 1.03E+00 | 8.86E+01 | 1.80E+02 | 3.90E+00 | 2.17E+02 |
| scs | 19.8 | 17.0 | 7.0 | 9.91E+00 | 9.23E-01 | 1.37E+00 | 2.19E-02 | 4.97E+01 | 1.23E+02 | 1.74E+00 | 5.21E+01 | 1.86E+02 | 3.10E+00 | 2.36E+02 |
| scs | 20.5 | 15.2 | 0.8 | 1.86E+01 | 1.76E+00 | 1.94E+00 | 3.10E-02 | 6.52E+01 | 1.08E+02 | 1.39E+00 | 1.48E+02 | 2.74E+02 | 5.70E+00 | 3.39E+02 |
| scs | 23.1 | 15.0 | 2.0 | 1.71E+01 | 1.90E+00 | 2.24E+00 | 3.58E-02 | 7.41E+01 | 1.21E+02 | 1.99E+00 | 1.26E+02 | 2.65E+02 | 5.77E+00 | 3.39E+02 |

Note: for species short names, see methods; DBH: diameter at breast height (cm), height: tree height (m), leaf: leaf biomass (kg), leaf sd: leaf biomass predictions standard deviation (kg), DAM: dead attached material biomass (kg), DAM sd: dead attached material biomass predictions standard deviation (kg), root: root biomass (kg)(no sd, see methods), stem: stem biomass (kg), stem sd: stem biomass predictions standard deviation (kg), branch wood: branch wood biomass (kg)(no sd because it was calculated later without error propagation, AGB: above-ground biomass (kg), ABG sd: above-ground biomass predictions standard deviation (kg), TB: total biomass (kg)(no sd, see methods)

Appendix 2: allometric equations

1) allometric equations for the minimal models predicting the leaf biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4, 3, 2, 2', 1 | *lnlf = - 4.432257 + 2.071974 x lndbh* |
| LM | All species | 4 | *lnlf = - 3.7973 + 2.1061 x lndbh - 1.4262 x lnH + 0.9193 x lnC + 2.4649 x WSG* |
| | | 3 | *lnlf = - 5.4053 + 2.3516 x lndbh - 0.7243 x lnH + 4.5249 x WSG* |
| | | 2 | *lnlf = - 3.6414 + 2.3541 x lndbh - 0.6002 x lnH* |
| | | 2' | *lnlf = - 6.00204 + 1.92160 x lndbh + 4.25905 x WSG* |
| | | 1 | *lnlf = - 4.22767 + 1.99402 x lndbh* |
| LME | Deciduous | 4, 3, 2 | *lnlf = - 6.627064 + 2.034349 x lndbh + 0.793464 x lnH* |
| | | 2', 1 | *lnlf = - 5.517087 + 2.419733 x lndbh* |
| LM | Deciduous | 4 | *lnlf = - 5.4348 + 1.8463 x lndbh + 0.6958 x lnC* |
| | | 3, 2, 2', 1 | *lnlf = - 5.3699 + 2.3486 x lndbh* |
| LME | Evergreen | 4, 3, 2, 2', 1 | *lnlf = - 3.478010 + 1.950953 x lndbh* |
| LM | Evergreen | 4, 3, 2' | *lnlf = - 5.28606 + 1.98327 x lndbh + 3.55187 x WSG* |
| | | 2, 1 | *lnlf = - 3.55084 + 1.99645 x lndbh* |
| LME | Coniferous | 4, 3, 2 | *lnlf = - 3.536499 + 2.407062 x lndbh - 1.068010 x lnH* |
| | | 2' | *lnlf = - 3.033957 + 1.916954 x lndbh - 4.353574 x WSG* |
| | | 1 | *lnlf = - 4.727695 + 1.893539 x lndbh* |
| LM | Coniferous | 4, 3 | *lnlf = - 2.8629 + 2.2014 x lndbh - 0.5665 x lnH - 3.2645 x WSG* |
| | | 2 | *lnlf = - 3.1743 + 2.5248 x lndbh - 1.3550 x lnH* |
| | | 2' | *lnlf = - 3.0340 + 1.9170 x lndbh - 4.3536 x WSG* |
| | | 1 | *lnlf = - 4.4017 + 1.7366 x lndbh* |
| LM | Alf | 3, 2, 1 | *lnlf = - 5.2852 + 2.3044 x lndbh* |

| | | | |
|---|---|---|---|
| LM | Lif | 3, 2, 1 | *lnlf = - 5.3427 + 2.4941 x lndbh* |
| LM | Sat | 3, 2 | *lnlf = - 10.7756 + 1.9215 x lndbh + 2.3143 x lnH* |
| | | 1 | *lnlf = - 6.2425 + 2.5660 x lndbh* |
| LM | Caf | 3, 2 | *lnlf = - 2.2947 + 2.4168 x lndbh - 0.8963 x lnH* |
| | | 1 | *lnlf = - 3.26482 + 1.93095 x lndbh* |
| LM | Cas | 3, 2, 1 | *lnlf = - 4.2660 + 2.2067 x lndbh* |
| LM | Scs | 3 | *lnlf = - 2.3124 + 2.1620 x lndbh - 1.5119 x lnH + 0.9821 x lnC* |
| | | 2, 1 | *lnlf = - 3.13020 + 1.84016 x lndbh* |
| LM | Cul | 3, 2, 1 | *lnlf = - 3.9617 + 1.6865 x lndbh* |
| LM | Pim | 3, 2, 1 | *lnlf = - 6.0857 + 2.3066 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnlf: log of leaf biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

2) allometric equations for the minimal models predicting the branch wood biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4 | *lnbr = - 6.941545 + 2.531856 x lndbh + 0.285025 x lnC + 5.094218 x WSG* |
| | | 3, 2’ | *lnbr = - 7.239649 + 2.746604 x lndbh + 5.720759 x WSG* |
| | | 2, 1 | *lnbr = - 4.687961 + 2.765076 x lndbh* |
| LM | All species | 4 | *lnbr = - 6.8603 + 2.4288 x lndbh + 0.3497 x lnC + 5.1794 x WSG* |
| | | 3, 2’ | *lnbr = - 7.17384 + 2.67619 x lndbh + 5.91398 x WSG* |
| | | 2, 1 | *lnbr = - 4.73705 + 2.78643 x lndbh* |
| LME | Deciduous | 4, 3, 2’, 2, 1 | *lnbr = - 5.076601 + 2.858220 x lndbh* |
| LM | Deciduous | 4 | *lnbr = - 7.2450 + 2.3434 x lndbh + 0.5622 x lnC + 5.2736 x WSG* |
| | | 3, 2’ | *lnbr = - 7.3571 + 2.7383 x lndbh + 5.7059 x WSG* |
| | | 2, 1 | *lnbr = - 5.1852 + 2.8827 x lndbh* |
| LME | Evergreen | 4 | *lnbr = - 3.623771 + 2.728276 x lndbh - 0.715259 x lnH + 0.602514 x lnC* |
| | | 3, 2, 2’, 1 | *lnbr = - 4.119904 + 2.696693 x lndbh* |
| LM | Evergreen | 4 | *lnbr = - 3.6335 + 2.7317 x lndbh - 0.7196 x lnH + 0.6099 x lnC* |
| | | 3, 2’ | *lnbr = - 6.09472 + 2.67638 x lndbh + 4.07836 x WSG* |
| | | 2, 1 | *lnbr = - 4.13503 + 2.70498 x lndbh* |
| LME | Coniferous | 4 | *lnbr = - 6.0379785 + 2.4167432 x lndbh + 0.3603437 x lnC + 3.1810964 x WSG* |
| | | 3, 2’ | *lnbr = - 6.489355 + 2.741452 x lndbh + 3.693587 x WSG* |
| | | 2, 1 | *lnbr = - 5.034633 + 2.753029 x lndbh* |
| LM | Coniferous | 4 | *lnbr = - 4.9374 + 2.5208 x lndbh - 1.1608 x lnH + 0.8113 x lnC + 4.7497 x WSG* |
| | | 3 | *lnbr = - 6.49756 + 2.73363 x lndbh + 0.01779 x lnH + 3.65972 x WSG* |
| | | 2 | *lnbr = - 6.3204 + 2.3921 x lndbh + 0.9538 x lnH* |
| | | 2’ | *lnbr = - 6.4894 + 2.7415 x lndbh + 3.6936 x WSG* |
| | | 1 | *lnbr = - 5.2912 + 2.8793 x lndbh* |
| LM | Alf | 3, 2, 1 | *lnbr = - 5.2321 + 2.7902 x lndbh* |
| LM | Lif | 3, 2, 1 | *lnbr = - 4.5149 + 2.8523 x lndbh* |

| | | | |
|---|---|---|---|
| LM | Sat | 3, 2 | *lnbr = - 9.0519 + 2.5246 x lndbh + 1.7111 x lnH* |
| | | 1 | *lnbr = - 5.7003 + 3.0010 x lndbh* |
| LM | Caf | 3 | *lnbr = - 2.2734 + 2.9556 x lndbh - 1.3665 x lnH + 0.4573 x lnC* |
| | | 2 | *lnbr = - 2.8769 + 3.0267 x lndbh - 0.8556 x lnH* |
| | | 1 | *lnbr = - 4.3183 + 2.7508 x lndbh* |
| LM | Cas | 3, 2, 1 | *lnbr = - 3.9534 + 2.5450 x lndbh* |
| LM | Scs | 3 | *lnbr = - 2.9906 + 2.7165 x lndbh - 1.6684 x lnH + 1.4725 x lnC* |
| | | 2, 1 | *lnbr = - 4.0237 + 2.7314 x lndbh* |
| LM | Cul | 3 | *lnbr = - 1.9674 + 3.5080 x lndbh - 3.0408 x lnH + 0.9723 x lnC* |
| | | 2, 1 | *lnbr = - 5.1868 + 2.6779 x lndbh* |
| LM | Pim | 3 | *lnbr = - 5.1645 + 2.2679 x lndbh + 0.1700 x lnH + 0.7396 x lnC* |
| | | 2 | *lnbr = - 6.7870 + 2.4809 x lndbh + 1.1107 x lnH* |
| | | 1 | *lnbr = - 4.8022 + 2.7842 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnbr: log of branch wood biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

3) allometric equations for the minimal models predicting the stem biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4 | *lnstem = - 4.272117 + 1.978162 x lndbh + 0.855795 x lnH - 0.145562 x lnC + 2.073982 x WSG* |
| | | 3 | *lnstem = - 4.004268 + 1.937548 x lndbh + 0.722839 x lnH + 1.842221 x WSG* |
| | | 2 | *lnstem = - 3.172565 + 1.942067 x lndbh + 0.719842 x lnH* |
| | | 2' | *lnstem = - 3.395134 + 2.308286 x lndbh + 2.386861 x WSG* |
| | | 1 | *lnstem = - 2.316230 + 2.309417 x lndbh* |
| LM | All species | 4, 3 | *lnstem = - 4.01469 + 1.91665 x lndbh + 0.76105 x lnH + 1.77133 x WSG* |
| | | 2 | *lnstem = - 3.35298 + 1.91591 x lndbh + 0.82258 x lnH* |
| | | 2' | *lnstem = - 3.3174 + 2.3277 x lndbh + 2.1248 x WSG* |
| | | 1 | *lnstem = - 2.44188 + 2.36729 x lndbh* |
| LME | Deciduous | 4, 3, 2 | *lnstem = - 3.232171 + 1.921179 x lndbh + 0.766637 x lnH* |
| | | 2', 1 | *lnstem = - 2.180150 + 2.301346 x lndbh* |
| LM | Deciduous | 4, 3 | *lnstem = - 4.03744 + 1.90670 x lndbh + 0.77148 x lnH + 1.85304 x WSG* |
| | | 2 | *lnstem = - 3.30057 + 1.96440 x lndbh + 0.74910 x lnH* |
| | | 2' | *lnstem = - 2.90069 + 2.28204 x lndbh + 1.72107 x WSG* |
| | | 1 | *lnstem = - 2.24557 + 2.32561 x lndbh* |
| LME | Evergreen | 4 | *lnstem = - 3.179471 + 2.057917 x lndbh + 0.842279 x lnH - 0.242194 x lnC* |
| | | 3, 2 | *lnstem = - 3.0474933 + 2.0268665 x lndbh + 0.6273195 x lnH* |
| | | 2', 1 | *lnstem = - 2.441925 + 2.391165 x lndbh* |
| LM | Evergreen | 4 | *lnstem = - 3.17947 + 2.05792 x lndbh + 0.84228 x lnH - 0.24219 x lnC* |
| | | 3, 2 | *lnstem = - 3.04749 + 2.02687 x lndbh + 0.62732 x lnH* |
| | | 2', 1 | *lnstem = - 2.45240 + 2.39591 x lndbh* |
| LME | Coniferous | 4 | *lnstem = - 4.2756735 + 1.9030914 x lndbh + 1.0607247 x lnH - 0.1774743 x lnC + 1.2428840 x WSG* |
| | | 3 | *lnstem = - 3.9343775 + 1.8565418 x lndbh + 0.8028916 x lnH + 1.4813388 x WSG* |
| | | 2 | *lnstem = - 3.430763 + 1.832871 x lndbh + 0.867771 x lnH* |
| | | 2' | *lnstem = - 3.563852 + 2.209588 x lndbh + 3.009887 x WSG* |

| | | | |
|---|---|---|---|
| | | 1 | *lnstem = - 2.367536 + 2.213671 x lndbh* |
| LM | Coniferous | 4 | *lnstem = - 4.27567 + 1.90309 x lndbh + 1.06072 x lnH - 0.17747 x lnC + 1.24288 x WSG* |
| | | 3 | *lnstem = - 3.93438 + 1.85654 x lndbh + 0.80289 x lnH + 1.48134 x WSG* |
| | | 2 | *lnstem = - 3.86268 + 1.71831 x lndbh + 1.18178 x lnH* |
| | | 2' | *lnstem = - 3.56385 + 2.20959 x lndbh + 3.00989 x WSG* |
| | | 1 | *lnstem = - 2.58747 + 2.32194 x lndbh* |
| LM | Alf | 3, 2 | *lnstem = - 2.80475 + 1.82700 x lndbh + 0.62757 x lnH* |
| | | 1 | *lnstem = - 1.91954 + 2.13178 x lndbh* |
| LM | Lif | 3, 2 | *lnstem = - 3.5936 + 1.8981 x lndbh + 0.9647 x lnH* |
| | | 1 | *lnstem = - 2.46426 + 2.45569 x lndbh* |
| LM | Sat | 3, 2 | *lnstem = - 3.4666 + 1.9960 x lndbh + 0.7863 x lnH* |
| | | 1 | *lnstem = - 1.9263 + 2.2149 x lndbh* |
| LM | Caf | 3 | *lnstem = - 2.83207 + 2.08770 x lndbh + 0.67488 x lnH - 0.24386 x lnC* |
| | | 2 | *lnstem = - 2.51025 + 2.04980 x lndbh + 0.40244 x lnH* |
| | | 1 | *lnstem = - 1.83229 + 2.17958 x lndbh* |
| LM | Cas | 3, 2 | *lnstem = - 3.0521 + 1.9297 x lndbh + 0.7233 x lnH* |
| | | 1 | *lnstem = - 2.51102 + 2.41774 x lndbh* |
| LM | Scs | 3, 2 | *lnstem = - 3.1161 + 2.0836 x lndbh + 0.5847 x lnH* |
| | | 1 | *lnstem = - 2.63543 + 2.45315 x lndbh* |
| LM | Cul | 3, 2 | *lnstem = - 3.4583 + 1.5556 x lndbh + 1.1207 x lnH* |
| | | 1 | *lnstem = - 2.86392 + 2.32615 x lndbh* |
| LM | Pim | 3, 2 | *lnstem = - 3.83099 + 1.83850 x lndbh + 1.07192 x lnH* |
| | | 1 | *lnstem = - 1.9155 + 2.1312 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnstem: log of stem wood biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

4) allometric equations for the minimal models predicting the dead attached material biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4, 3, 2, 2', 1 | *lndam = - 7.739322 + 2.360095 x lndbh* |
| LM | All species | 4, 3, 2' | *lndam = - 10.5624 + 2.3531 x lndbh + 6.1131 x WSG* |
| | | 2, 1 | *lndam = - 8.0156 + 2.4571 x lndbh* |
| LME | Deciduous | 4, 3, 2, 2', 1 | *lndam = - 7.852738 + 2.166646 x lndbh* |
| LM | Deciduous | 4, 3, 2' | *lndam = - 17.1186 + 2.4361 x lndbh + 19.4624 x WSG* |
| | | 2, 1 | *lndam = - 9.7102 + 2.9287 x lndbh* |
| LME | Evergreen | 4, 3, 2, 2', 1 | *lndam = - 7.560284 + 2.345912 x lndbh* |
| LM | Evergreen | 4, 3, 2, 2', 1 | *lndam = - 7.1503 + 2.0913 x lndbh* |
| LME | Coniferous | 4, 3, 2 | *lndam = - 11.981462 + 1.667456 x lndbh + 2.913095 x lnH* |
| | | 2', 1 | *lndam = - 7.954220 + 2.761602 x lndbh* |
| LM | Coniferous | 4, 3, 2 | *lndam = - 10.5896 + 1.5036 x lndbh + 2.4826 x lnH* |
| | | 2' | *lndam = - 10.5412 + 2.6576 x lndbh + 7.0040 x WSG* |
| | | 1 | *lndam = - 8.3408 + 2.9477 x lndbh* |
| LM | Alf | 3, 2, 1 | *lndam = - 4.6672* |
| LM | Lif | 3, 2, 1 | *lndam = - 9.7483 + 2.8536 x lndbh* |
| LM | Sat | 3, 2, 1 | *lndam = - 6.3463 + 2.2156 x lndbh* |
| LM | Caf | 3, 2, 1 | *lndam = - 9.3677 + 2.4943 x lndbh* |
| LM | Cas | 3, 2, 1 | *lndam = - 5.0213 + 1.5203 x lndbh* |
| LM | Scs | 3, 2, 1 | *lndam = - 7.5627 + 2.6120 x lndbh* |
| LM | Cul | 3, 2, 1 | *lndam = - 8.7533 + 2.8759 x lndbh* |
| LM | Pim | 3 | *lndam = - 6.1366 + 3.2329 x lndbh - 1.4867 x lnC* |
| | | 2, 1 | *lndam = - 6.2542 + 2.2884 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lndam: log of dead attached material biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

5) allometric equations for the minimal models predicting the root biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4, 3, 2 | *lnroot = - 2.7679791 + 2.5605396 x lndbh - 0.5297173 x lnH* |
| | | 2', 1 | *lnroot = - 3.331234 + 2.263259 x lndbh* |
| LM | All species | 4 | *lnroot = - 3.6676 + 2.4499 x lndbh - 0.5281 x lnH + 0.1424 x lnC + 1.9746 x WSG* |
| | | 3 | *lnroot = - 3.9167 + 2.4879 x lndbh - 0.4194 x lnH + 2.2937 x WSG* |
| | | 2 | *lnroot = - 3.0225 + 2.4892 x lndbh - 0.3565 x lnH* |
| | | 2' | *lnroot = - 4.26223 + 2.23898 x lndbh + 2.13980 x WSG* |
| | | 1 | *lnroot = - 3.37076 + 2.27537 x lndbh* |
| LME | Deciduous | 4, 3, 2, 2', 1 | *lnroot = - 3.801700 + 2.495886 x lndbh* |
| LM | Deciduous | 4 | *lnroot = - 4.6105 + 2.3979 x lndbh - 0.7233 x lnH + 0.5106 x lnC + 4.3633 x WSG* |
| | | 3, 2' | *lnroot = - 5.77811 + 2.40465 x lndbh + 4.87963 x WSG* |
| | | 2, 1 | *lnroot = - 3.92068 + 2.52817 x lndbh* |
| LME | Evergreen | 4, 3, 2 | *lnroot = - 2.5259100 + 2.6943672 x lndbh - 0.7339077 x lnH* |
| | | 2', 1 | *lnroot = - 3.147793 + 2.234245 x lndbh* |
| LM | Evergreen | 4, 3, 2 | *lnroot = - 2.4955 + 2.7072 x lndbh - 0.7613 x lnH* |
| | | 2', 1 | *lnroot = - 3.13561 + 2.22678 x lndbh* |
| LME | Coniferous | 4, 3, 2, 2', 1 | *lnroot = - 3.072636 + 1.992817 x lndbh* |
| LM | Coniferous | 4, 3, 2, 2', 1 | *lnroot = - 3.0726 + 1.9928 x lndbh* |
| LM | Alf | 3, 2, 1 | *lnroot = - 4.0164 + 2.4728 x lndbh* |
| LM | Lif | 3, 2, 1 | *lnroot = - 2.9647 + 2.3319 x lndbh* |
| LM | Sat | 3, 2, 1 | *lnroot = - 5.134 + 2.923 x lndbh* |
| LM | Caf | 3, 2 | *lnroot = - 1.5885 + 3.0954 x lndbh - 1.5822 x lnH* |
| | | 1 | *lnroot = - 3.3010 + 2.2378 x lndbh* |
| LM | Cas | 3, 2, 1 | *lnroot = - 2.7386 + 2.0151 x lndbh* |
| LM | Scs | 3, 2, 1 | *lnroot = - 3.1950 + 2.3343 x lndbh* |
| LM | Cul | 3, 2, 1 | *lnroot = - 2.4580 + 1.7086 x lndbh* |

| | | | |
|---|---|---|---|
| LM | Pim | 3, 2 | *lnroot = - 6.1601 + 2.3111 x lndbh + 0.9242 x lnH* |
| | | 1 | *lnroot = - 4.5085 + 2.5635 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnroot: log of root biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

6) allometric equations for the minimal models predicting the total aboveground biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4 | *lnTAB = - 3.553819 + 2.120642 x lndbh + 0.273563 x lnH + 0.070273 x lnC + 2.782854 x WSG* |
| | | 3 | *lnTAB = - 3.685385 + 2.140158 x lndbh + 0.331833 x lnH + 2.932185 x WSG* |
| | | 2 | *lnTAB = - 2.378688 + 2.139610 x lndbh + 0.341790 x lnH* |
| | | 2’ | *lnTAB = - 3.424276 + 2.327556 + lndbh + 3.128309 x WSG* |
| | | 1 | *lnTAB = - 2.013607 + 2.330586 x lndbh* |
| LM | All species | 4 | *lnTAB = - 3.40426 + 2.09231 x lndbh + 0.21271 x lnH + 0.14651 x lnC + 2.63384 x WSG* |
| | | 3 | *lnTAB = - 3.66052 + 2.13142 x lndbh + 0.32457 x lnH + 2.96213 x WSG* |
| | | 2 | *lnTAB = - 2.50581 + 2.13307 x lndbh + 0.40581 x lnH* |
| | | 2’ | *lnTAB = - 3.39312 + 2.32409 x lndbh + 3.08124 x WSG* |
| | | 1 | *lnTAB = - 2.10944 + 2.37649 x lndbh* |
| LME | Deciduous | 4, 3, 2 | *lnTAB = - 3.110423 + 2.066583 x lndbh + 0.688273 x lnH* |
| | | 2’, 1 | *lnTAB = - 2.155015 + 2.403663 x lndbh* |
| LM | Deciduous | 4 | *lnTAB = - 3.95608 + 2.00209 x lndbh + 0.57962 x lnH + 0.12144 x lnC + 2.35456 x WSG* |
| | | 3 | *lnTAB = - 4.15470 + 2.02979 x lndbh + 0.69799 x lnH + 2.46817 x WSG* |
| | | 2 | *lnTAB = - 3.17322 + 2.10664 x lndbh + 0.66818 x lnH* |
| | | 2’ | *lnTAB = - 3.1263 + 2.3694 x lndbh + 2.3488 x WSG* |
| | | 1 | *lnTAB = - 2.23219 + 2.42883 x lndbh* |
| LME | Evergreen | 4, 3, 2, 2’, 1 | *lnTAB = - 1.906932 + 2.358592 x lndbh* |
| LM | Evergreen | 4, 3, 2, 2’, 1 | *lnTAB = - 1.92015 + 2.36686 x lndbh* |
| LME | Coniferous | 4, 3 | *lnTAB = - 3.2768648 + 2.0394385 x lndbh + 0.3213889 x lnH + 2.2442834 x WSG* |
| | | 2, 1 | *lnTAB = - 2.045275 + 2.206039 x lndbh* |
| | | 2’ | *lnTAB = - 3.179839 + 2.200788 x lndbh + 2.862117 x WSG* |
| LM | Coniferous | 4, 3 | *lnTAB = - 3.2769 + 2.0394 x lndbh + 0.3214 x lnH + 2.2443 x WSG* |
| | | 2 | *lnTAB = - 3.0628 + 1.8171 x lndbh + 0.8635 x lnH* |
| | | 2’ | *lnTAB = - 3.17984 + 2.20079 x lndbh + 2.86212 x WSG* |

| | | | |
|---|---|---|---|
| | | 1 | *lnTAB = - 2.28068 + 2.31936 x lndbh* |
| LM | Alf | 3, 2 | *lnTAB = - 2.56212 + 2.01383 x lndbh + 0.45202 x lnH* |
| | | 1 | *lnTAB = - 1.92452 + 2.23336 x lndbh* |
| LM | Lif | 3, 2 | *lnTAB = - 3.0616 + 2.2252 x lndbh + 0.5895 x lnH* |
| | | 1 | *lnTAB = - 2.37136 + 2.56600 x lndbh* |
| LM | Sat | 3, 2 | *lnTAB = - 3.89318 + 2.08686 x lndbh + 0.94220 x lnH* |
| | | 1 | *lnTAB = - 2.0476 + 2.3492 x lndbh* |
| LM | Caf | 3, 2, 1 | *lnTAB = - 1.76313 + 2.31409 x lndbh* |
| LM | Cas | 3, 2, 1 | *lnTAB = - 2.00052 + 2.36124 x lndbh* |
| LM | Scs | 3 | *lnTAB = - 1.9827 + 2.1762 x lndbh + 0.2805 x lnC* |
| | | 2, 1 | *lnTAB = - 1.92110 + 2.38102 x lndbh* |
| LM | Cul | 3, 2, 1 | *lnTAB = - 2.20388 + 2.16346 x lndbh* |
| LM | Pim | 3, 2 | *lnTAB = - 3.69711 + 1.99616 x lndbh + 0.98049 x lnH* |
| | | 1 | *lnTAB = - 1.94498 + 2.26390 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnTAB: log of total above - ground biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

7) allometric equations for the minimal models predicting the total biomass

| Type | Species/group of species | Pred. | Allometric equation |
|---|---|---|---|
| LME | All species | 4, 3 | *lnTB = - 3.197794 + 2.187917 x lndbh + 0.196454 x lnH + 2.805399 x WSG* |
| | | 2 | *lnTB = - 1.9441225 + 2.1879709 x lndbh + 0.2041593 x lnH* |
| | | 2’ | *lnTB = - 3.043347 + 2.298679 x lndbh + 2.922765 x WSG* |
| | | 1 | *lnTB = - 1.726070 + 2.302055 x lndbh* |
| LM | All species | 4 | *lnTB = - 2.93301 + 2.13741 x lndbh + 0.09100 x lnH + 0.14146 x lnC + 2.49755 x WSG* |
| | | 3 | *lnTB = - 3.18045 + 2.17518 x lndbh + 0.19901 x lnH + 2.81454 x WSG* |
| | | 2 | *lnTB = - 2.08328 + 2.17674 x lndbh + 0.27620 x lnH* |
| | | 2’ | *lnTB = - 3.01650 + 2.29331 x lndbh + 2.88757 x WSG* |
| | | 1 | *lnTB = - 1.81350 + 2.34241 x lndbh* |
| LME | Deciduous | 4, 3, 2 | *lnTB = - 2.723610 + 2.137118 x lndbh + 0.560576 x lnH* |
| | | 2’, 1 | *lnTB = - 1.943959 + 2.411161 x lndbh* |
| LM | Deciduous | 4 | *lnTB = - 3.67390 + 2.04019 x lndbh + 0.37545 x lnH + 0.20315 x lnC + 2.86083 x WSG* |
| | | 3 | *lnTB = - 4.00618 + 2.08654 x lndbh + 0.57346 x lnH + 3.05089 x WSG* |
| | | 2 | *lnTB = - 2.7930 + 2.1815 x lndbh + 0.5366 x lnH* |
| | | 2’ | *lnTB = - 3.1612 + 2.3655 x lndbh + 2.9528 x WSG* |
| | | 1 | *lnTB = - 2.03722 + 2.44028 x lndbh* |
| LME | Evergreen | 4, 3, 2, 2’, 1 | *lnTB = - 1.630284 + 2.329931 x lndbh* |
| LM | Evergreen | 4, 3, 2’ | *lnTB = - 2.42167 + 2.32900 x lndbh + 1.60355 x WSG* |
| | | 2, 1 | *lnTB = - 1.63827 + 2.33495 x lndbh* |
| LME | Coniferous | 4, 3, 2’ | *lnTB = - 2.520075 + 2.126656 x lndbh + 2.182837 x WSG* |
| | | 2, 1 | *lnTB = - 1.664889 + 2.135525 x lndbh* |
| LM | Coniferous | 4, 3 | *lnTB = - 2.54246 + 2.08943 x lndbh + 0.07414 x lnH + 2.04030 x WSG* |
| | | 2 | *lnTB = - 2.3479 + 1.8873 x lndbh + 0.5670 x lnH* |
| | | 2’ | *lnTB = - 2.52007 + 2.12666 x lndbh + 2.18284 x WSG* |
| | | 1 | *lnTB = - 1.83432 + 2.21709 x lndbh* |

| | | | |
|---|---|---|---|
| LM | Alf | 3, 2, 1 | *lnTB = - 1.82727 + 2.27869 x lndbh* |
| LM | Lif | 3, 2 | *lnTB = - 2.9350 + 2.0255 x lndbh + 0.8406 x lnH* |
| | | 1 | *lnTB = - 1.95093 + 2.51134 x lndbh* |
| LM | Sat | 3, 2 | *lnTB = - 3.6019 + 2.2181 x lndbh + 0.7785 x lnH* |
| | | 1 | *lnTB = - 2.0769 + 2.4349 x lndbh* |
| LM | Caf | 3, 2, 1 | *lnTB = - 1.5203 + 2.2882 x lndbh* |
| LM | Cas | 3, 2, 1 | *lnTB = - 1.62163 + 2.28292 x lndbh* |
| LM | Scs | 3, 2, 1 | *lnTB = - 1.66266 + 2.37096 x lndbh* |
| LM | Cul | 3, 2, 1 | *lnTB = - 1.6378 + 2.0270 x lndbh* |
| LM | Pim | 3, 2 | *lnTB = - 3.59922 + 2.03070 x lndbh + 0.96823 x lnH* |
| | | 1 | *lnTB = - 1.8690 + 2.2951 x lndbh* |

Note: model type is either a linear model (LM) or a mixed linear model (LME), for the species names see METHODS, Pred: number of predictors of the initial models. lnTB: log of total biomass (kg), lndbh: log of diameter at breast height (cm), lnH: log of tree height (m), lnC: log of crown length (m), WSG: wood specific gravity (g $cm^{-3}$)

# GENERAL DISCUSSION

In this thesis, I have extended BEF studies to the canopy of a species-rich subtropical forest. Although canopies have already received a considerable amount of attention as reservoirs of biodiversity (Erwin 1982; Allison et al. 1993; Lowman & Wittman 1996), little has been done to investigate the effects of tree species richness on the arthropod communities and on the levels of herbivory damage (Cardinale et al. 2011). In the first two chapters, I could show that tree species richness did influence arthropod communities and herbivory. I could also detect effects of other factors, such as stand age and date at which arthropods were collected. However, it is worth noting how difficult it can be to draw definitive conclusions from observational studies like this one because potentially confounding factors can be linked with the main variable of interest, tree species richness. Nevertheless, my results are valuable because it is not possible to build experiments capable of mimicking the whole complexity of real conditions (Leuschner et al. 2009). In this regard, observational studies are fundamental to control if conclusions drawn from simple systems remain valid in complex, natural ecosystems.

*Herbivory and plant species richness*

Along the gradient of tree species richness present in our plots, we found a positive effect of tree species richness and phylogenetic diversity on levels of herbivory. Tree species richness and tree phylogenetic diversity were strongly correlated with each other, making their effects on herbivory exchangeable in our models. However, there was still enough orthogonality to find a significant interaction between these two terms. Phylogenetic diversity was a mediator of the effect of tree species richness, as can be seen in figure 4 of chapter 1. At low levels of phylogenetic diversity, additional tree species in the plots increase damage from herbivory; at high levels of phylogenetic diversity the opposite trend was

observed. This result supports different hypotheses that rely on resource dilution as main explanatory factor. This result also implies that a part of the arthropod community was to a certain degree specialized on feeding on particular plant species. More precisely, the interaction suggests that the effects of resource dilution are effective on arthropod populations only if the resources are different enough (high phylogenetic diversity). In this regard, Bertheau et al. (2010) showed that the fitness of specialist herbivores decreased as the phylogenetic distance between the herbivore-preferred host and the available host increased. In contrast, adding similar plant species in the plot increased herbivory damage because it could have reduced or annihilated the dilution effect on specialist herbivores, or it could have benefited the generalist herbivores through a diet improvement. The latter situation is predicted by the "dietary mixing hypothesis" (after Bernays et al. 1994), which postulates that generalist herbivores increase their fitness by consuming a varied mix of plant species. Interestingly, we did not observe any effects of tree species composition, as revealed by our multivariate analyses performed with Nonmetric Multidimensional Scaling. The lack of effects of plant species composition suggests a generic action of plant species richness and phylogenetic diversity that goes beyond a sampling effect. For instance, different studies reported an effect of plant species identity on levels of herbivory damage (reviewed by Jactel & Brockerhoff 2007). Because phylogenetic diversity is a direct consequence of the identity of the species in a plot, the effects of species identity might have been hidden phylogenetic diversity effects. The mediating effect of plant phylogenetic diversity on herbivory damage has only recently been included in BEF studies (Jactel & Brockerhoff 2007; Dinnage 2013; Castagneyrol et al. 2014; Schuldt et al. 2014). In this chapter, we were the first to show the existence of a phylogenetic diversity effect on herbivory levels in the canopy layer of a species-rich subtropical forest. Another important

bottom-up hypothesis that we could not exclude was the “more individuals hypothesis” (Wright 1983; Srivastava & Lawton 1998), which predicts an increased herbivore abundance in plots with more biomass available. Although we did not see a direct effect of plot total leaf biomass on herbivory damage, the plot aboveground biomass is related to tree species richness (Baruffol et al. 2013). For an equal level of herbivory, plots with greater leaf biomass would also suffer greater total biomass loss. Therefore, it is possible that plot with higher tree species richness suffered from higher total biomass loss. Finally, opposed to the two aforementioned bottom-up hypotheses, the top-down hypotheses predict that a higher plant species richness provides better conditions for the predators (for example: shelters or temporal prey availability), resulting in a stronger predator impact on herbivore abundances. Such top-down control of herbivores, however, was not supported by our findings.

*Potential implications for future BEF studies*

One of our most noticeable results regarding BEF was certainly the effect of tree species relative leaf biomass, which is the relative contribution of one species to the total leaf biomass of the plot, on the level of herbivory, because this implied a density–dependent mechanism. However, our results were in the opposite direction than predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971) and by the “resource dilution hypothesis” (Root 1973). In our plots, rare species in terms of leaf biomass suffered higher herbivory damage than more common species. Plath et al. (2011) explained a similar situation by the fact that specialist arthropods tended to accumulate more on their hosts when the latter were diluted. In addition, we also showed that the different tree species suffered from various levels of herbivory caused by different arthropod feeding guilds. The

different feeding guilds were also differentially sensitive to tree relative leaf biomass, tree species richness, and tree phylogenetic diversity.

In this light, we formulate a hypothesis to reconcile our results with the Janzen-Connell hypothesis. We suggest that the altered proportions of herbivory caused by the different feeding guilds in response to resource dilution could be more important in modifying the plant's fitness than the levels of total herbivory damage *per se*. We further postulate that a key to improve the understanding of density-dependent BEF mechanisms might be the inclusion of phylogenetic diversity as explanatory variable. Because fully polyphagous or strict monophagous arthropods should not be sensitive to phylogenetic diversity in its strict sense but only to species richness, Dinnage (2013) introduced the term of "cladophage" consumers. Cladophage consumers are defined as the consumers feeding on a group of phylogenetically related species. Such a group must be sensitive to the phylogenetic diversity by definition. Thus, we suggest that they potentially have a large role in our study site because we could detect the effect of phylogenetic diversity. Additionally, Dinnage (2013) cites the work of Yguel et al. (2011) that found that oak trees growing among phylogenetically distant individuals experienced lower herbivory damage than oaks growing among closely related individuals. Such a result suggests a density-dependent mechanisms relying on the phylogenetic distance among individuals of different species whereas the Janzen-Connell hypothesis was originally postulated as a density-dependent mechanisms for co-occurring conspecific individuals. Because the observed levels of herbivory have already been shown to impact plant seed production and viability (Marquis 1988; Smith & Hough-Goldstein 2014), reduce plant growth (Zvereva et al. 2012; Kim et al. 2013), and modify species composition through altered seedling recruitment (Bagchi et al. 2014), density-dependent mechanisms that change the levels of herbivory or the proportion of damages

done by the different feeding guilds have the potential to contribute to maintaining plant species diversity.

Regarding future investigations, I suggest to include more rigorous examination of the phylogeny of the hosts. For instance, the phylogeny of the tree species could be used to construct a “phylogenetic index” of the different species. This index would be characterised by a phylogenetic average and a phylogenetic distance from this average for each tree species in each plot. Such an index would describe if one species is in a phylogenetic extremity (i.e. phylogenetic isolation) compared to the other species or close to the phylogenetic average of the plot. As an illustration, imagine a plot with four species of oaks, one species of beech, and one species of pine. Here, it appears clear that the plot phylogenetic average is situated among the oak species phylogenetic values, and that the phylogenetic extremity is represented by the pine. This index could be weighted by abundance or not. This index could be used to specifically address former unresolved questions about the underlying mechanisms by which host phylogeny, phylogenetic diversity, and plant species richness interact with herbivores. For instance, concerning the mediating role of phylogenetic diversity on species richness effects, we expect to find less herbivory damage on species that are phylogenetically isolated because these species would experience a true dilution. The previous results of Yguel et al. (2011) and my own results reporting lower herbivory damage on *Pinus massoniana* tend to support this hypothesis. An extension of this hypothetical framework could mix the spatial distribution of the trees with the phylogenetic index to see how the physical distance among related or unrelated individuals affects the herbivory damage.

*Arthropods and plant species richness*

In chapter two, we reported arthropod patterns generally consistent with a bottom-up situation; in particular, we did not find patterns that would have been expected according to predictions of top-down hypotheses.

The abundance of the whole arthropod community was related to tree species richness. However, tree species richness was not related to the species richness of arthropods. This allowed us to exclude hypotheses predicting an increase of arthropod abundance as a consequence of the increase of arthropod species richness, as in the "resource specialization hypothesis" (Hutchinson 1959; Strong et al. 1984; Siemann et al. 1998), the "stability hypothesis" (Hutchinson 1959), and the "niche hypothesis" (MacArthur 1972). Additionally, the "resource specialization hypothesis" was further not supported because there was no link between arthropod and plant species compositions. Altogether, these patterns indicated that the "more individual hypothesis" was most likely the main driving force in our system. Taken separately, the feeding guild abundances did not show a link with the plant species richness: only when they were summed the link was significant. Because the different feeding guilds might be sensible to different factors that covary with tree species richness, it is foreseeable that each feeding guild responded indirectly to the tree species richness, thus preventing us to detect a link.

*Prey-predators links*

Predator arthropods were quantitatively (abundance and species richness) and qualitatively (species composition) related to their potential prey (herbivore, pollinator, and detritivore arthropods). These different links led us to select the "more individual hypothesis", the "resources specialization hypothesis", and the "niche hypothesis" as the most likely

candidate hypotheses governing predator populations. These hypotheses are bottom-up hypotheses, meaning that the predator populations were driven by prey availability and identity. These hypotheses also imply that at least a part of the predator community was specialized with regard to its food source. In contrast, we did not detect an effect of tree species composition on herbivore patterns. This lack of links pointed toward a high degree of generalism for the herbivores. Hence, we rejected in chapter two the “niche hypothesis” and the “resources specialization hypothesis”. In addition, the positive relationship between herbivores and predators led us to exclude a top-down control such as would have been predicted by the “enemy hypothesis”.

However, as we previously pointed out considering the herbivory damage, an important part of the herbivores could have been cladophage. Indeed, considering cladophagy could reconcile the apparent lack of tree species composition effect on herbivore populations. For example, two common tree species present in our plots, *Castanopsis eyrei* and *Castanopsis fargesii*, belong to the same genus. The tree species composition analysis will consider these two species as independent. As a result, an arthropod feeding on these two species would not be detected as influenced by the tree species composition. However, if the phylogenetic identity of those trees could be included, for example using the phylogenetic index that I previously suggested, then effects of tree species phylogenetic composition may appear. These considerations enhance the advice we previously gave about future research directions. Indeed, we think that the tree phylogeny has the potential of being a keystone in explaining herbivore arthropod distributions and the resulting herbivory. In addition, obtaining tree phylogenetic data does not require an excessive workload in comparison to improving the arthropod data. The arthropods we collected were separated by species but without identifying the real species identity. This procedure, already very time consuming,

plus the observation of the mouthparts, allowed us to classify the arthropods into morphospecies grouped into feeding guilds. To refine these data, the arthropod real species identity (i.e. not morphospecies) would be required. Such a procedure is extremely difficult when several thousand specimens have been collected. Furthermore, only a handful people in the world would have the knowledge to do this. They would require a tremendous amount of time probably unaffordable for any research group.

Two additional factors that potentially blurred the link between tree species composition and trapped herbivore arthropods were: 1) the potential bias of the trapping system and 2) the fact that pollinators were not counted as herbivores although pollinators are herbivores in the first stage of their life. Since the traps we used might have captured comparatively more external feeders, which are on average more often generalist (Novotny & Basset 2005), we may have biased the sampled population toward generalism. Additionally, the non-inclusion of the pollinators as herbivore arthropods could have increased the bias, although making an educated guess on this effect appears difficult.

*Combining arthropod populations and herbivory damage*

Pearson correlations between the different herbivory damages and arthropod abundances provided some additional insights about which feeding guild was the most probably responsible one for the herbivory damage but also revealed some incongruities in the expected patterns.

The first intriguing result is that total herbivore abundance was not correlated with total herbivory damage. This could put into question how we grouped the different herbivore groups (folivores, sap-suckers, and miscellaneous) into a single herbivore feeding guild. The

separate feeding guilds also did not correlate with the total damage. It is interesting to note that the chewer damage, which represented two thirds of the total damage, was not explained by the folivore feeding guild. In contrast, the skeletonizer damage correlated with the folivore and the miscellaneous abundances. How can we explain such a surprising pattern? First, it is possible that some of the leaves that I recorded as chewed were in fact skeletonized. The skeletonizer arthropods eat the mesophyll and the upper or the lower leaf epidermis. Then, the remaining epidermis dries and falls off after a while. Subsequently, the old skeletonized parts of the leaf appear as chewed. Therefore, the damage recognized as skeletonized is certain while the damage recognized as chewed could be misidentified. Second some fungi might have destroyed part of the leaf surface that could have been afterward counted as chewed. Remarkably, the damage for which we have the greatest certitude, the skeletonized leaves, also displayed the best correlations with the different herbivore feeding guilds. The predator feeding guild did not show any particular link with herbivory damage except for a positive correlation between the predator abundance and the sap-feeding damage. Such a pattern is consistent with the conclusions of chapter one and two: there was no top-down control of herbivore arthropods or herbivory damage in our species-rich forest.

The lack of top-down control of herbivores also contradicts the “green world hypothesis” (Hairston et al. 1960), stating that predators prevent the plants to be completely defoliated by controlling herbivore populations. If no top-down control regulates the herbivore populations, what prevents them from being more abundant? Species-rich subtropical or tropical forests offer resource stability and diversity, which is hypothesized to facilitate the development of herbivore arthropods. Therefore, we need a better understanding of the different bottom-up mechanisms. Concerning future research, I advise to follow the same

direction that I suggested previously: to include the plant phylogenetic identity to see if it matches with the arthropod species composition. From the observations we have made in chapter one and two, we expect to find links between the plant phylogenetic identity and the arthropod species composition. Such links would also be consistent with the concept of cladophagy that we previously explained.

Table 1. Correlations (Pearson, n = 27) between herbivory damage and arthropod abundance. The folivore, sap-sucker, and miscellaneous groups constitute the herbivore groups. Significances are marked with stars (* p<0.05, ** p<0.01, *** p<0.001).

| Damage → / Arthropod ↓ | Total damage | Chewed | Skeletonized | Sap-feeding damages | Undefined damages |
|---|---|---|---|---|---|
| Total abundance | 0.27 | 0.14 | 0.45* | 0.15 | 0.05 |
| Herbivore abundance | 0.03 | 0.03 | 0.25 | -0.03 | -0.11 |
| Folivore abundance | 0.55** | 0.29 | 0.63*** | 0.19 | 0.26 |
| Sap-sucker abundance | -0.05 | 0.06 | -0.11 | -0.11 | -0.08 |
| Miscellaneous abundance | 0.06 | -0.03 | 0.50** | 0.06 | -0.11 |
| Pollinator abundance | 0.16 | 0.24 | 0.19 | -0.13 | -0.13 |
| Detritivore abundance | 0.32 | 0.07 | 0.43* | 0.30 | 0.25 |
| Predator abundance | -0.01 | -0.24 | 0.11 | 0.48* | 0.04 |

Because many of the relationships we have described were rather weak, and the explanative power of our models was rather low, we also suggest extending the duration of future trophic studies. Indeed, our study was done within a short time period, hence only representing a “snapshot” at this precise moment. However, it has been shown that

arthropod populations can be dynamic: a bottom-up configuration can even switch to a top-down configuration within the season (Gratton & Denno 2003). Therefore, it would be advisable to perform a continuous arthropod survey, and this for two reasons: first, if the arthropod patterns change during the season, we would be able to detect it, and second, as plant species diversity may affect arthropod species turnover (Haddad et al. 2009), the sum of the samples collected during a continuous survey could be converted into cumulative abundances, which would give us the ability to detect alteration in species turnover.

*Tree allometry*

The allometry chapter, chapter 3, was mostly motivated by the need to have reliable biomass equations for the tree individuals of this area. Because the proportions of a tree change with its size, we showed the pertinence of having a different set of models for each biomass compartment. As a result of our investigations for the best final models, we showed how the final form of these models depended on tree species identity or on the group of species modelled, on the type of model (linear model (LM) or mixed-effect linear model (LME)) and, most importantly, on the biomass compartment that was predicted. The results showed that, on average, the more species that were included in the model the more predictors were necessary for a good prediction. Mixed-effect linear models were less sensitive to extreme values and therefore to be preferred for biomass predictions of trees not belonging to the focal species. Looking from a physiological point of view, the comparison between LM and LME models gave us insights about the relative importance of predictors: the predictors that were retained in LME models were characterised by a general relationship with biomass that held across the eight species. In this regard, we reported the diameter at breast height (DBH) and the wood specific gravity (WSG) to be the two most

important predictors. They are also the two predictors the most worthy to be acquired from a cost-benefit perspective. In contrast, tree height and crown length are worthy of being measured only if detailed predictions at the species level have to be made. Consequently, we advise to measure only the DBH and the WSG. We also advise to use species-specific LM models when the predictions have to be made for trees belonging to the same species as the one used to fit the allometric model, and to use mixed-species LME models when the predictions have to be done for trees of different species or groups of trees also containing different species than the ones used to fit the allometric model. Finally, one of our main findings was that the variability of the predicted biomass compartments increased in the following sequence: stem > total biomass > total aboveground biomass > roots > branch wood > leaves > dead attached material.

Next, we used one of the selected models to predict the whole tree biomass of our study plots (CSPs). We showed how plot prediction variability depended on the number of trees within the plot because individual errors compensate for each other. Meanwhile, the correctness of the overall prediction also depended on the bias, which introduced a systematic error on each tree. The bias is a direct consequence of the DBH evenness of the trees used to build the model. We also used these models to calculate the leaf biomass of the study plots (CSPs) and used this estimated leaf biomass as covariable in chapter one. Total plot leaf biomass was considered as a good proxy for resource availability for the arthropods. The models were also used to calculate relative leaf biomass, which is the relative contribution of one species to the total plot leaf biomass, as a proxy for the isolation experienced by the different tree species. Previously, the basal area has been used an approximation of resource availability for arthropods (Schuldt et al. 2010). Though basal area was correlated with our estimated leaf biomass, sharing 91% of variability, coniferous

and broadleaved trees were characterized by a different relationship between their DBH and their leaf biomass: the coniferous species have a lower leaf biomass for a given diameter at breast height. Therefore, because we used distinct models for coniferous and broadleaves, the leaf biomass of plots having a lot of coniferous species was not over-estimated.

**General conclusion**

Both the arthropod and the herbivory damage patterns concurred with a general bottom-up situation regarding the arthropod communities. We also detected different density-dependent mechanisms and explored some options about how these mechanisms could influence the plant community and help in maintaining the extraordinary plant biodiversity found in this subtropical forest. Our study adds to other recent studies (Riihimäki et al. 2005; Schuldt et al. 2011; Zhang & Adams 2011) that questioned the importance of a top-down control in species-rich established forests. It is worth noting that a large grassland experiment, the Jena Experiment, also described similar bottom-up controls (Scherber et al. 2010). Furthermore, the absence of a top-down control underlines our general lack of comprehension of the main mechanisms regulating arthropod herbivory. The median herbivory damage that we recorded on our leaves was only 2.5 %. Consequently, a large amount of resource would still have been available for consumption by herbivores. Understanding what keeps the world green and promotes biodiversity is not yet complete and promises years of fascinating research! Big projects, for example BEF–China, have the huge advantage of being comprehensive. Instead of trying to put together the results of many different small BEF studies, each one working on their own sub-topic of the subject, a

project like BEF–China investigates each aspect of BEF in a coordinated framework. Because, for example, soil microbial respiration and leaf allometry, despite their apparent independence, might have to be analysed together to be fully understood, we need large, integrated BEF projects that enable us to join such separated areas of biodiversity and ecosystem research. Projects like BEF–China or the Jena Experiment are our best chance to uncover the intimacy of biodiversity–ecosystem functioning.

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